ON MECHANICAL SELECTION AND OTHER PROBLEMS.

By KARL JORDAN, Dr. Phil.

[Plates XVI., XVII., XVIII., and XIX].

THE peculiar kind of variation I have to deal with in this paper concerns some accessory organs of the reproductive system of a group of insects, and bears closely upon Romanes's theory of Physiological Selection. It is *a priori* evident that the demonstration of the occurrence of an extensive variability in any part of those organs which are the most important for the preservation of animated nature must be of far-reaching consequence in respect to the origin of species. As the mere statement of the facts would be unintelligible to the general reader who has no special knowledge of the animals in question, I shall endeavour to interpret the facts. However, before I begin to give the details, it is necessary to come to an understanding about some questions of a general character, and this necessitates my entering, rather reluctantly, upon a ground which nowadays has so often been traversed, with and without success: I should not do so, if the facts I bring forth, and the conclusions I have to derive from them, did not put me in contraposition to a good many naturalists. Being surrounded by cabinets full of specimens, I shall, during this excursion on a theoretical ground, always be reminded that possibilities arrived at by general reasoning are often impossibilities in nature, in so far as what is *a priori* possible or even probable may be found not to occur in nature.

I.—INTRODUCTORY NOTES.

Everybody who is a little acquainted with the diagnostic works on Zoology or Botany will know sufficiently that a continuous question of contest amongst us species-makers is whether a given form of animal or plant is a "distinct species" or not; and he will also have become aware that in many cases the contending parties do not come to an understanding, because, though using the same term "species," the mutual conception of that term is widely different. And this is so not only amongst us species-makers, but we meet with the phenomenon also in the essays of a more philosophical kind which bear upon the theory of evolution. It would almost appear, in fact, as if a "species" is that which a respective author chooses to consider a "species." It is not necessary to give any illustration taken from systematic works, first, since we do not think it does much harm to the value of purely diagnostic articles whether the term "species" is always applied in the same sense by the same or various authors; secondly, because illustrations can be found in any volume containing descriptions of varieties and species. In natural philosophy, however, so far as it endeavours to explain by theories the diversities in animated nature, it is all important that an author has a fixed idea of that diversity which he in his writings calls a "species," and therefore we will give here an illustration of the before-mentioned phenomenon taken from this side of our science.

In a short article in which he claims priority over Romanes with regard to physiological selection, Dahl* proceeds to say that a separation of the varieties of one species into more species within the same locality is not possible, if the various

---

* *Zool. Anzeiger* 1889. p. 262.

ON MECHANICAL SELECTION AND OTHER PROBLEMS.

BY KARL JORDAN, DR. PHIL.

[Plates XVI., XVII., XVIII., and XIX].

THE peculiar kind of variation I have to deal with in this paper concerns some accessory organs of the reproductive system of a group of insects, and bears closely upon Romanes's theory of Physiological Selection. It is *a priori* evident that the demonstration of the occurrence of an extensive variability in any part of those organs which are the most important for the preservation of animated nature must be of far-reaching consequence in respect to the origin of species. As the mere statement of the facts would be unintelligible to the general reader who has no special knowledge of the animals in question, I shall endeavour to interpret the facts. However, before I begin to give the details, it is necessary to come to an understanding about some questions of a general character, and this necessitates my entering, rather reluctantly, upon a ground which nowadays has so often been traversed, with and without success: I should not do so, if the facts I bring forth, and the conclusions I have to derive from them, did not put me in contraposition to a good many naturalists. Being surrounded by cabinets full of specimens, I shall, during this excursion on a theoretical ground, always be reminded that possibilities arrived at by general reasoning are often impossibilities in nature, in so far as what is *a priori* possible or even probable may be found not to occur in nature.

I.—INTRODUCTORY NOTES.

Everybody who is a little acquainted with the diagnostic works on Zoology or Botany will know sufficiently that a continuous question of contest amongst us species-makers is whether a given form of animal or plant is a "distinct species" or not; and he will also have become aware that in many cases the contending parties do not come to an understanding, because, though using the same term "species," the mutual conception of that term is widely different. And this is so not only amongst us species-makers, but we meet with the phenomenon also in the essays of a more philosophical kind which bear upon the theory of evolution. It would almost appear, in fact, as if a "species" is that which a respective author chooses to consider a "species." It is not necessary to give any illustration taken from systematic works, first, since we do not think it does much harm to the value of purely diagnostic articles whether the term "species" is always applied in the same sense by the same or various authors; secondly, because illustrations can be found in any volume containing descriptions of varieties and species. In natural philosophy, however, so far as it endeavours to explain by theories the diversities in animated nature, it is all important that an author has a fixed idea of that diversity which he in his writings calls a "species," and therefore we will give here an illustration of the before-mentioned phenomenon taken from this side of our science.

In a short article in which he claims priority over Romanes with regard to physiological selection, Dahl* proceeds to say that a separation of the varieties of one species into more species within the same locality is not possible, if the various varieties did not possess, besides the (morphological) distinguishing characters, either antipathy against mutual intercrossing, or mutual sterility, or both qualities; and he gives the following illustration :—

---

* *Zool. Anzeiger* 1889. p. 262.

"The caterpillars of the two closely allied species of butterflies *Gonopteryx rhamni* and *G. cleopatra* became adapted to different species of plants, the one to *Rhamnus frangula* [and *cathartica*], the other to *Rhamnus alpina*, *i.e.* the apparatus of digestion became so modified that those species of plants could be made use of [physiologically] in the best possible manner. With the condition of the organs of digestion was associated, perhaps indirectly, a somewhat different yellow colour in the imago-state, and here the preference could begin to act. . . . Against a thousand butterflies adapted to *Rhamnus alpina* there occurred perhaps two which were prepossessed in favour of a deeper yellow colour, two which preferred a lighter yellow tint, while those thousand were indifferent [to the deeper or lighter tint of yellow]. The first-named [two] specimens copulated with individuals adapted to *Rhamnus alpina*, and gave birth only to fully fertile offspring. The second group [two specimens] copulated with light-coloured individuals adapted to *Rhamnus frangula*, and gave birth to non-fertile intergraduates. Of the thousand specimens one half copulated with specimens adapted to *Rhamnus alpina*, the other half with specimens adapted to *Rhamnus frangula* ; of the two halves, therefore, only the first gave birth to fully fertile offspring. . . . It is easily to be seen that the number of those individuals which were prepossessed in favour of closely allied specimens [in colour] would grow very quickly, and that the number of the others must very soon become reduced, even if this number at the beginning [of the selection] is still more preponderating [than in the above illustration]."

As the author expressly states that the divarication of species at the same locality is not possible if together with the "*development of the distinguishing characters* there did not take place *a development of dislike*," etc., we must take it as the meaning of the illustration that *Gonopteryx rhamni* and *G. cleopatra* have developed from a common ancestor into two species by means of psychological selection. Or, to put it figuratively, the species A developed into two varieties, A^1 and A^2, in consequence of the caterpillars becoming changed by the influence of the different food-plants; then psychological selection on the part of some females set in and modified those two varieties more and more, so that the varieties A^1 and A^2 became in the course of time two "species" B and C. Which characters does the author attribute to the two varieties A^1 and A^2 at the time when selection commenced to act? There were four distinguishing characters: (1) A^1 and A^2 were different in the chemistry of their body; (2) they were so different in colour that the *females* could perceive the difference; (3) A^1 produced only pale specimens, and A^2 only deeper-coloured specimens, *i.e.* they bred true; (4) the cross-products were not fit to propagate. Now, if forms so widely distinguished morphologically and physiologically as A^1 and A^2 are not "species," then we fear there are no species at all. The author apparently confounds the transmutation of one species into one other and the separation of a species into two or more. The illustration does not show how by means of psychological selection (or any other modifying factor) *G. cleopatra* and *G. rhamni* have in the same locality developed from one common ancestor into two species, but shows how the two "species" *cleopatra* and *rhamni* might become the one a paler and paler, the other a deeper and deeper yellow "species." At the time when selection set in in Dahl's illustration there were already two "species," and hence the specific distinctness of the two is not the outcome of psychological selection.

varieties did not possess, besides the (morphological) distinguishing characters, either antipathy against mutual intercrossing, or mutual sterility, or both qualities; and he gives the following illustration :—

"The caterpillars of the two closely allied species of butterflies *Gonopteryx rhamni* and *G. cleopatra* became adapted to different species of plants, the one to *Rhamnus frangula* [and *cathartica*], the other to *Rhamnus alpina*, *i.e.* the apparatus of digestion became so modified that those species of plants could be made use of [physiologically] in the best possible manner. With the condition of the organs of digestion was associated, perhaps indirectly, a somewhat different yellow colour in the imago-state, and here the preference could begin to act. . . . Against a thousand butterflies adapted to *Rhamnus alpina* there occurred perhaps two which were prepossessed in favour of a deeper yellow colour, two which preferred a lighter yellow tint, while those thousand were indifferent [to the deeper or lighter tint of yellow]. The first-named [two] specimens copulated with individuals adapted to *Rhamnus alpina*, and gave birth only to fully fertile offspring. The second group [two specimens] copulated with light-coloured individuals adapted to *Rhamnus frangula*, and gave birth to non-fertile intergraduates. Of the thousand specimens one half copulated with specimens adapted to *Rhamnus alpina*, the other half with specimens adapted to *Rhamnus frangula*; of the two halves, therefore, only the first gave birth to fully fertile offspring. . . . It is easily to be seen that the number of those individuals which were prepossessed in favour of closely allied specimens [in colour] would grow very quickly, and that the number of the others must very soon become reduced, even if this number at the beginning [of the selection] is still more preponderating [than in the above illustration]."

As the author expressly states that the divarication of species at the same locality is not possible if together with the "*development of the distinguishing characters* there did not take place *a development of dislike*," etc., we must take it as the meaning of the illustration that *Gonopteryx rhamni* and *G. cleopatra* have developed from a common ancestor into two species by means of psychological selection. Or, to put it figuratively, the species *A* developed into two varieties, A^1 and A^2, in consequence of the caterpillars becoming changed by the influence of the different food-plants; then psychological selection on the part of some females set in and modified those two varieties more and more, so that the varieties A^1 and A^2 became in the course of time two "species" *B* and *C*. Which characters does the author attribute to the two varieties A^1 and A^2 at the time when selection commenced to act? There were four distinguishing characters: (1) A^1 and A^2 were different in the chemistry of their body; (2) they were so different in colour that the *females* could perceive the difference; (3) A^1 produced only pale specimens, and A^2 only deeper-coloured specimens, *i.e.* they bred true; (4) the cross-products were not fit to propagate. Now, if forms so widely distinguished morphologically and physiologically as A^1 and A^2 are not "species," then we fear there are no species at all. The author apparently confounds the transmutation of one species into one other and the separation of a species into two or more. The illustration does not show how by means of psychological selection (or any other modifying factor) *G. cleopatra* and *G. rhamni* have in the same locality developed from one common ancestor into two species, but shows how the two "species" *cleopatra* and *rhamni* might become the one a paler and paler, the other a deeper and deeper yellow "species." At the time when selection set in in Dahl's illustration there were already two "species," and hence the specific distinctness of the two is not the outcome of psychological selection.

In order to avoid similar confusion we have to come to a conclusion which definition of the term "species" as opposed to the lower degrees of variation we will accept, before we discuss the variability of the genital armature within the limits of a "species."

As most of us pretend to be evolutionists, let us take it as an axiom, which we need not discuss here any more, that the great divergency exhibited in animated nature is the result of the development of the various forms of animals and plants from a common ancestor. Before Darwin brought forward his theory of evolution naturalists had to solve one question: which are the differences found to exist among the various forms of animals and plants? The question which is put to naturalists nowadays is, however, twofold: (1) which kinds of divergency do we find to exist in nature? (2) how has this divergency come about?

It seems to us to be a rather general assumption amongst naturalists, no matter whether they treat animated nature from the point of view of a philosopher, or whether they work with the individual specimens, that the variation of the individuals which belong to a complex called species is such that, with the exception of marked di- and polymorphism, we can draw up a series of specimens which form a continuous chain from one extreme variety to the other, the differences between the adjoining links being extremely slight. And it is almost natural that the assumption should be so general. The question which governs zoological work is one of specific differences on the side of us systematists, and one of the causes of the specific and non-specific characters on the side of the biologists, and over the consideration of "characters" it has been lost sight of that speaking of a specific character and the variability of characters means, in fact, speaking of *abstracta*, while our work must be based upon *concreta*, upon the individual specimens. The variation of an organ may be continuous; in a series of individuals a certain organ may even be constant; but that does by no means imply that the individuals as opposed to one of their organs form a continuous chain. An individual has many "characters," and these do not vary in the same manner and degree in the various specimens; some individuals may be almost identical in one or some characters, while they are widely different in other respects, and this will at once become manifest to everybody who actually tries to put together a "continuous" series of specimens. An illustration will bring the fact more closely to mind. A, B, C, D may represent individuals; a, b, c, three characters; a^1, a^2, a^3, a^4, etc., b^1, b^2, etc., c^1, c^2, c^3, etc., may be minute degrees of development of the characters. Now, if we arrange the individuals according to the gradual development of the character a, and thus have a continuous series in respect to this character, the chain of individuals will nevertheless be discontinuous, as in the following diagram:—

$$\begin{array}{lllll} A & B & C & D & \dots \\ a^1 & a^2 & a^3 & a^4 & \dots \\ b^{10} & b^1 & b^6 & b^{15} & \dots \\ c^1 & c^2 & c^7 & c^3 & \dots \\ \vdots & \vdots & \vdots & \vdots & \end{array}$$

If we further arrange the series according to the continuity of character b or c, not only will the individuals A, B, C . . . stand in other places within the new series, but also new individuals must be introduced to make the chain again continuous. Hence it will be sufficiently clear that, notwithstanding the variation of every organ of a species may be continuous, the individuals each being a sum of organs

In order to avoid similar confusion we have to come to a conclusion which definition of the term "species" as opposed to the lower degrees of variation we will accept, before we discuss the variability of the genital armature within the limits of a "species."

As most of us pretend to be evolutionists, let us take it as an axiom, which we need not discuss here any more, that the great divergency exhibited in animated nature is the result of the development of the various forms of animals and plants from a common ancestor. Before Darwin brought forward his theory of evolution naturalists had to solve one question: which are the differences found to exist among the various forms of animals and plants? The question which is put to naturalists nowadays is, however, twofold: (1) which kinds of divergency do we find to exist in nature? (2) how has this divergency come about?

It seems to us to be a rather general assumption amongst naturalists, no matter whether they treat animated nature from the point of view of a philosopher, or whether they work with the individual specimens, that the variation of the individuals which belong to a complex called species is such that, with the exception of marked di- and polymorphism, we can draw up a series of specimens which form a continuous chain from one extreme variety to the other, the differences between the adjoining links being extremely slight. And it is almost natural that the assumption should be so general. The question which governs zoological work is one of specific differences on the side of us systematists, and one of the causes of the specific and non-specific characters on the side of the biologists, and over the consideration of "characters" it has been lost sight of that speaking of a specific character and the variability of characters means, in fact, speaking of *abstracta*, while our work must be based upon *concreta*, upon the individual specimens. The variation of an organ may be continuous; in a series of individuals a certain organ may even be constant; but that does by no means imply that the individuals as opposed to one of their organs form a continuous chain. An individual has many "characters," and these do not vary in the same manner and degree in the various specimens; some individuals may be almost identical in one or some characters, while they are widely different in other respects, and this will at once become manifest to everybody who actually tries to put together a "continuous" series of specimens. An illustration will bring the fact more closely to mind. A, B, C, D may represent individuals; a, b, c, three characters; a^1, a^2, a^3, a^4, etc., b^1, b^2, etc., c^1, c^2, c^3, etc., may be minute degrees of development of the characters. Now, if we arrange the individuals according to the gradual development of the character a, and thus have a continuous series in respect to this character, the chain of individuals will nevertheless be discontinuous, as in the following diagram:—

$$\begin{array}{lllll}
A & B & C & D & \ldots \\
a^1 & a^2 & a^3 & a^4 & \ldots \\
b^{10} & b^1 & b^6 & b^{15} & \ldots \\
c^1 & c^2 & c^7 & c^3 & \ldots \\
\vdots & \vdots & \vdots & \vdots &
\end{array}$$

If we further arrange the series according to the continuity of character b or c, not only will the individuals A, B, C . . . stand in other places within the new series, but also new individuals must be introduced to make the chain again continuous. Hence it will be sufficiently clear that, notwithstanding the variation of every organ of a species may be continuous, the individuals each being a sum of organs form a discontinuous series. We can express this phenomenon in other words as the law of *independent variation* of organs as opposed to the *correlative variation* of organs.

There are many species in which not only the individuals form discontinuous series, but which exhibit also one or more discontinuously variable characters; and it is especially the appearance of such discontinuity which Bateson so amply illustrates in *Materials for the Study of Variation* (London, 1894). In this case the specimens belonging to a species can be arranged into groups according to a discontinuous character, each group containing individuals in which that character is continuous or nearly so, while from one group to the other that character exhibits a more or less wide gap. In diagnostic zoology the groups of individuals of polymorphic animals have often been mistaken for distinct species. The study of independent discontinuous variation of two or more organs can, however, often help us to distinguish polymorphism from specific distinctness. In the following diagram the specimens are first arranged into groups according to character a, and then into groups according to character b:—

$$\begin{array}{lccc|ccc}
\text{I.} & A & B & C & D & E & F \\
 & a^1 & a^2 & a^3 & a^7 & a^8 & a^9 \\
 & b^8 & b^9 & b^1 & b^2 & b^3 & b^7 \\
 & c^{14} & c^7 & c^6 & c^5 & c^9 & c^{12} \\
 & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
 & & & & & & \\
\text{II.} & C & D & E & A & H & I \\
 & b^1 & b^2 & b^3 & b^8 & b^9 & b^{10} \\
 & a^3 & a^7 & a^8 & a^1 & a^{11} & a^{12} \\
 & c^6 & c^5 & c^9 & c^{14} & c^2 & c^3 \\
 & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots
\end{array}$$

In the first arrangement (I.) $A\ B\ C$ form one, $D\ E\ F$ another group; in the second arrangement $C\ D\ E$ belong to one, and $A\ H\ I$ to another. In each case the individuals $A\ B\ C\ D\ E\ F\ H\ I$ form two groups not connected by intergradations, each group, therefore, being conformable to what we species-makers call "species" as a rule; but in the first arrangement the specimen C belongs together with A and B to a "species," while in the second arrangement it stands together with D and E, which, according to arrangement I., are specifically different from A, B, and C. The danger of arriving at erroneous results by taking into account only one organ is so evident and so well known that one must wonder how it is possible that nevertheless a classification—for example, of *Lepidoptera*—based upon wing-markings alone, or upon neuration, can be expected to be an exact expression of the blood-relationship of the classified forms.

Which characters are correlated and which independent in respect to variation can only be found out by the study of individual variation; where this study is neglected correlated characters are often taken to be independent diagnostic characters. The length of the wing and the breadth of the wing-bands are often correlated in *Lepidoptera*, and so is in many cases the lesser or greater concavity of the outer margin of the forewing of butterflies depending on the length of the wing; to say in such cases that a certain form of butterfly differs from another form in the wing being longer, externally more concave and having narrower bands, would amount to the same as if in the case of two black forms with yellow spots we should say that the one is differentiated from the other by the yellow spots being restricted and by the black ground-colour being extended.

form a discontinuous series. We can express this phenomenon in other words as the law of *independent variation* of organs as opposed to the *correlative variation* of organs.

There are many species in which not only the individuals form discontinuous series, but which exhibit also one or more discontinuously variable characters; and it is especially the appearance of such discontinuity which Bateson so amply illustrates in *Materials for the Study of Variation* (London, 1894). In this case the specimens belonging to a species can be arranged into groups according to a discontinuous character, each group containing individuals in which that character is continuous or nearly so, while from one group to the other that character exhibits a more or less wide gap. In diagnostic zoology the groups of individuals of polymorphic animals have often been mistaken for distinct species. The study of independent discontinuous variation of two or more organs can, however, often help us to distinguish polymorphism from specific distinctness. In the following diagram the specimens are first arranged into groups according to character a, and then into groups according to character b:—

$$\begin{array}{lccc|ccc}
\text{I.} & A & B & C & D & E & F \\
 & a^1 & a^2 & a^3 & a^7 & a^8 & a^9 \\
 & b^8 & b^9 & b^1 & b^2 & b^3 & b^7 \\
 & c^{14} & c^7 & c^6 & c^5 & c^9 & c^{12} \\
 & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots \\
 & & & & & & \\
\text{II.} & C & D & E & A & H & I \\
 & b^1 & b^2 & b^3 & b^8 & b^9 & b^{10} \\
 & a^3 & a^7 & a^8 & a^1 & a^{11} & a^{12} \\
 & c^6 & c^5 & c^9 & c^{14} & c^2 & c^3 \\
 & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots
\end{array}$$

In the first arrangement (I.) *A B C* form one, *D E F* another group; in the second arrangement *C D E* belong to one, and *A H I* to another. In each case the individuals *A B C D E F H I* form two groups not connected by intergradations, each group, therefore, being conformable to what we species-makers call "species" as a rule; but in the first arrangement the specimen *C* belongs together with *A* and *B* to a "species," while in the second arrangement it stands together with *D* and *E*, which, according to arrangement I., are specifically different from *A*, *B*, and *C*. The danger of arriving at erroneous results by taking into account only one organ is so evident and so well known that one must wonder how it is possible that nevertheless a classification—for example, of *Lepidoptera*—based upon wing-markings alone, or upon neuration, can be expected to be an exact expression of the blood-relationship of the classified forms.

Which characters are correlated and which independent in respect to variation can only be found out by the study of individual variation; where this study is neglected correlated characters are often taken to be independent diagnostic characters. The length of the wing and the breadth of the wing-bands are often correlated in *Lepidoptera*, and so is in many cases the lesser or greater concavity of the outer margin of the forewing of butterflies depending on the length of the wing; to say in such cases that a certain form of butterfly differs from another form in the wing being longer, externally more concave and having narrower bands, would amount to the same as if in the case of two black forms with yellow spots we should say that the one is differentiated from the other by the yellow spots being restricted and by the black ground-colour being extended.

The independent variability of organs found to exist among the individuals derived from one *female*, or among the individuals flying in the same locality—in short, among specimens about the specific identity of which there is no doubt—leads us to the conclusion that the same organs of the same species vary also independently in other localities. The distinguishing characters of a geographical race thus can be shown to be independent of one another, and that the association of distinguishing characters is not correlation of these characters, which is of the greatest importance, if we come to consider the causes of the divergence exhibited by such races, the degree of relationship of the races, and the probable history of their geographical distribution. We mention in this place only that, as the wing-form and wing-pattern of the *Papilios* vary independently of the copulatory organs, we shall find in the body of this paper ample illustrations of those three phylogenetical and biological phenomena. The first we have to do is in every case to study the individual variation in order to know which characters are correlated and which not in respect to variation, then to study the characters of the same organs of the geographical representatives of the same species, and finally to compare the results we arrive at, if we draw from each single independent character conclusions as to subspecific and specific distinctness, the influence of the evolutionistic factors, and the history of this influence.

The occasional appearance of individuals, mostly single or in very small numbers, amongst the normal specimens, differing widely from the latter in one or more points, we have to classify as a peculiar kind of di- and polymorphism. The so-called sports and monstrosities, between which terms there is no line of delimitation, as there is also no such line between normal and abnormal varieties, belong to this kind of discontinuous variation, and it is a rather general assumption that the characters of such sports and monstrosities get swamped away by intercrossing. Is this really true in the verbal sense? If swamped away means "not appearing in the direct offspring" of that abnormal specimen, it might often be correct; but if it means disappearing for ever, never reappearing amongst the individuals constituting the species, it is not true. Many sports and even monstrosities are found again and again, as every collector knows; and when an exceptionally abnormal variety has been found once, there is no reason for the assumption that it will not be found a second time. In fact, the collectors, who work with individuals, expect and hope to come across such a variety themselves. If, for example, somebody had published this year that from one of his pupae of *Acherontia atropos* (death-head moth) a specimen with entirely ochreous wings had emerged, we are quite sure that all those who are in possession of a considerable number of pupae of this insect would look forward to the emergence of the imagines with the eager expectation to find such an individual among them.*

The repeated occurrence of the same abnormal variety is, to our mind, of the greatest importance, as the repetition of the phenomenon is a proof that the variety, how abnormal and rare it ever may be, is not entirely swamped away from the species, and that the constitution of the individuals of the respective species, taken as a whole, is such that under certain circumstances, whichever they may be, the variety will be produced, or even must be produced. It is, therefore, quite intelligible that, when those certain circumstances become more frequent, the variety which we now call abnormal might become normal. From this point of view, the record of unusual varieties, including monstrosities, is by no means so unimportant as it appears to be to the systematist who recognises only "distinct" species. On the contrary, we

---

* For illustrations see Bateson, *Materials for the Study of Variation.* London, 1894.

The independent variability of organs found to exist among the individuals derived from one *female*, or among the individuals flying in the same locality—in short, among specimens about the specific identity of which there is no doubt—leads us to the conclusion that the same organs of the same species vary also independently in other localities. The distinguishing characters of a geographical race thus can be shown to be independent of one another, and that the association of distinguishing characters is not correlation of these characters, which is of the greatest importance, if we come to consider the causes of the divergence exhibited by such races, the degree of relationship of the races, and the probable history of their geographical distribution. We mention in this place only that, as the wing-form and wing-pattern of the *Papilios* vary independently of the copulatory organs, we shall find in the body of this paper ample illustrations of those three phylogenetical and biological phenomena. The first we have to do is in every case to study the individual variation in order to know which characters are correlated and which not in respect to variation, then to study the characters of the same organs of the geographical representatives of the same species, and finally to compare the results we arrive at, if we draw from each single independent character conclusions as to subspecific and specific distinctness, the influence of the evolutionistic factors, and the history of this influence.

The occasional appearance of individuals, mostly single or in very small numbers, amongst the normal specimens, differing widely from the latter in one or more points, we have to classify as a peculiar kind of di- and polymorphism. The so-called sports and monstrosities, between which terms there is no line of delimitation, as there is also no such line between normal and abnormal varieties, belong to this kind of discontinuous variation, and it is a rather general assumption that the characters of such sports and monstrosities get swamped away by intercrossing. Is this really true in the verbal sense? If swamped away means "not appearing in the direct offspring" of that abnormal specimen, it might often be correct; but if it means disappearing for ever, never reappearing amongst the individuals constituting the species, it is not true. Many sports and even monstrosities are found again and again, as every collector knows; and when an exceptionally abnormal variety has been found once, there is no reason for the assumption that it will not be found a second time. In fact, the collectors, who work with individuals, expect and hope to come across such a variety themselves. If, for example, somebody had published this year that from one of his pupae of *Acherontia atropos* (death-head moth) a specimen with entirely ochreous wings had emerged, we are quite sure that all those who are in possession of a considerable number of pupae of this insect would look forward to the emergence of the imagines with the eager expectation to find such an individual among them.*

The repeated occurrence of the same abnormal variety is, to our mind, of the greatest importance, as the repetition of the phenomenon is a proof that the variety, how abnormal and rare it ever may be, is not entirely swamped away from the species, and that the constitution of the individuals of the respective species, taken as a whole, is such that under certain circumstances, whichever they may be, the variety will be produced, or even must be produced. It is, therefore, quite intelligible that, when those certain circumstances become more frequent, the variety which we now call abnormal might become normal. From this point of view, the record of unusual varieties, including monstrosities, is by no means so unimportant as it appears to be to the systematist who recognises only "distinct" species. On the contrary, we maintain with Eimer that abnormal varieties show distinctly the directions in which a species is able to develop. We give an illustration. For certain reasons which we cannot explain here, as they concern details of structure, we must consider *Papilio sarpedon* to be derived from a form which had green spots within the cell of the forewing and a submarginal row of green markings, and that *P. sarpedon* is now on the way to lose the green markings altogether. The specimens of *P. sarpedon* from the Solomon Islands have preserved some of the additional spots, while in the forms from other localities the forewing has only a median macular band; in South India and Ceylon the first spot of this band disappears very often, and in China the band of the hindwing is often reduced to a costal patch. Now, Mr. de Nicéville figures a "sport" from Sumatra * in which the median band of both wings has disappeared, except a small spot, and which therefore has an almost entirely black upperside. The specimen is now in the Tring Museum, which contains also another individual of *P. sarpedon* (from Sikkim) that has the median band of the forewing dusted over with black scales, which conceal partly the green ground-colour of the wing-membrane. The direction of development indicated by these two "sports" coincides with that which we are led by structural characters to consider the real direction of development of *P. sarpedon*, and the importance of this coincidence is obvious.

---

* For illustrations see Bateson, *Materials for the Study of Variation*. London, 1894.

Apart from polymorphism among the individuals in the same locality, we observe very commonly a polymorphism in which the various forms are separated geographically. This geographical polymorphism we shall have to deal with later on, and therefore we restrict ourselves here to the remark that the various geographical varieties are, just like the forms of ordinary polymorphism, often not connected by intergradations, and thus are likely to mislead us species-makers to treat them as "distinct species"; in the latter respect geographical and non-geographical polymorphism have much in common, because they are homologous phenomena, as we shall soon see; and we may add that geographical separation of different forms cannot be an *a priori* criterion of specific distinctness, though this has often enough been alleged.

The individual variation including non-geographical and geographical polymorphism, as dealt with in the preceding lines, concerns especially the individuals which exist as contemporaries; now let us briefly consider the historical side of the variation. According to the theory of evolution, the descendants have in the course of time (gradually or *per saltum*, in respect to the distinguishing characters as well as to time) become dissimilar to their ancestors; we assume generally that a long period was necessary to bring a considerable change in an animal or plant about. A period of one or two hundred years is by many systematists considered quite insufficient to alter in nature a form of animal or plant so far that the change is obvious, or that any transformation has taken place at all within the same locality. Though we accept the theory of the transmutation of the species in the course of time as the base of scientific work in Natural History, we nevertheless *identify* the forms found in our days with the forms which our forefathers in science had before them; without hesitation we treat the forms, whether they be species or variety, captured in 1896, as identical with those which Linné received a hundred and fifty years ago, or which Merian or Seba obtained about two hundred years back. And when we observe a difference between our recent specimens and the old pictures, differences which are by no means always explainable by the assumption of incorrectness of the drawings, maintain with Eimer that abnormal varieties show distinctly the directions in which a species is able to develop. We give an illustration. For certain reasons which we cannot explain here, as they concern details of structure, we must consider *Papilio sarpedon* to be derived from a form which had green spots within the cell of the forewing and a submarginal row of green markings, and that *P. sarpedon* is now on the way to lose the green markings altogether. The specimens of *P. sarpedon* from the Solomon Islands have preserved some of the additional spots, while in the forms from other localities the forewing has only a median macular band; in South India and Ceylon the first spot of this band disappears very often, and in China the band of the hindwing is often reduced to a costal patch. Now, Mr. de Nicéville figures a "sport" from Sumatra * in which the median band of both wings has disappeared, except a small spot, and which therefore has an almost entirely black upperside. The specimen is now in the Tring Museum, which contains also another individual of *P. sarpedon* (from Sikkim) that has the median band of the forewing dusted over with black scales, which conceal partly the green ground-colour of the wing-membrane. The direction of development indicated by these two "sports" coincides with that which we are led by structural characters to consider the real direction of development of *P. sarpedon*, and the importance of this coincidence is obvious.

---

* *Journ. Bombay N. H. Soc.* 1893, p. 54, t. I, f. 11 (♂).

Apart from polymorphism among the individuals in the same locality, we observe very commonly a polymorphism in which the various forms are separated geographically. This geographical polymorphism we shall have to deal with later on, and therefore we restrict ourselves here to the remark that the various geographical varieties are, just like the forms of ordinary polymorphism, often not connected by intergradations, and thus are likely to mislead us species-makers to treat them as "distinct species"; in the latter respect geographical and non-geographical polymorphism have much in common, because they are homologous phenomena, as we shall soon see; and we may add that geographical separation of different forms cannot be an *a priori* criterion of specific distinctness, though this has often enough been alleged.

The individual variation including non-geographical and geographical polymorphism, as dealt with in the preceding lines, concerns especially the individuals which exist as contemporaries; now let us briefly consider the historical side of the variation. According to the theory of evolution, the descendants have in the course of time (gradually or *per saltum*, in respect to the distinguishing characters as well as to time) become dissimilar to their ancestors; we assume generally that a long period was necessary to bring a considerable change in an animal or plant about. A period of one or two hundred years is by many systematists considered quite insufficient to alter in nature a form of animal or plant so far that the change is obvious, or that any transformation has taken place at all within the same locality. Though we accept the theory of the transmutation of the species in the course of time as the base of scientific work in Natural History, we nevertheless *identify* the forms found in our days with the forms which our forefathers in science had before them; without hesitation we treat the forms, whether they be species or variety, captured in 1896, as identical with those which Linné received a hundred and fifty years ago, or which Merian or Seba obtained about two hundred years back. And when we observe a difference between our recent specimens and the old pictures, differences which are by no means always explainable by the assumption of incorrectness of the drawings, the very last we think of in systematic work is that the form we now receive from a particular locality has actually changed during the last fifty or two hundred years. Of course, our knowledge of a single specimen of a certain form preserved from the collections made during the last century, and our knowledge of an old figure of that form, does not enable us to draw any conclusions as to the extent of variation of that form at the time of its capture, nor does such poor knowledge admit any conclusion as to a probable transformation. The evidence is gone, and that is very much to be regretted.[*] But should not the want of evidence from the past be a hint to us to procure more evidence for the scientists who come after us? It is all important to prove that the transmutation of species upon which the theory of evolution is based actually takes place; and it would be a good object for small provincial museums to preserve long series of specimens, with exact dates, at least of the species of those families of the respective district which are known to be easily influenced by the transmutating factors, families which moreover are easily preserved, such as butterflies and moths, wingless beetles, and landshells; museums with such collections would not be simply a sight for the public, but they would be of scientific value, and their scientific success would be far superior to that which they can obtain by gathering sparse material from all countries of the globe. There would certainly be no want of voluntary help from the side of private collectors in civilised countries. The study of the local fauna and flora and their variation carried out in this sense, though many systematists and species-makers (which terms are not always synonymous) look down upon the study of aberrations as being unscientific, stands far above the mere descriptions of new species, which mostly do not help the least to solve the all-governing questions of evolution, but add simply some more "species" to the hundreds of thousands of "species" already made known.

---

* *Journ. Bombay N. H. Soc.* 1893, p. 54, t. I, f. 11 (♂).

However, we are not entirely left without evidence that transformation is actually going on under our eyes. We know from many plants[†] and a small number of animals that geographical races, when reared under conditions other than those of the country where the race lives, change in characters; we refer to the Porto Santo rabbits,[‡] and *Polyommatus phlaeas*,[§] and *Pieris brassicae*.[‖] And a striking the very last we think of in systematic work is that the form we now receive from a particular locality has actually changed during the last fifty or two hundred years. Of course, our knowledge of a single specimen of a certain form preserved from the collections made during the last century, and our knowledge of an old figure of that form, does not enable us to draw any conclusions as to the extent of variation of that form at the time of its capture, nor does such poor knowledge admit any conclusion as to a probable transformation. The evidence is gone, and that is very much to be regretted.* But should not the want of evidence from the past be a hint to us to procure more evidence for the scientists who come after us? It is all important to prove that the transmutation of species upon which the theory of evolution is based actually takes place; and it would be a good object for small provincial museums to preserve long series of specimens, with exact dates, at least of the species of those families of the respective district which are known to be easily influenced by the transmutating factors, families which moreover are easily preserved, such as butterflies and moths, wingless beetles, and landshells; museums with such collections would not be simply a sight for the public, but they would be of scientific value, and their scientific success would be far superior to that which they can obtain by gathering sparse material from all countries of the globe. There would certainly be no want of voluntary help from the side of private collectors in civilised countries. The study of the local fauna and flora and their variation carried out in this sense, though many systematists and species-makers (which terms are not always synonymous) look down upon the study of aberrations as being unscientific, stands far above the mere descriptions of new species, which mostly do not help the least to solve the all-governing questions of evolution, but add simply some more "species" to the hundreds of thousands of "species" already made known.

---

[*] Since the above was written I have received Oberthür's *Études d'Entomologie* XX. 1896. Here Oberthür tries to demonstrate from copies of old figures of *Lepidoptera* and figures of recently caught specimens that no change has taken place in these insects since Linné's time. The differences, however, which are exhibited by these old drawings and the figures of the recent specimens are not only so conspicuous that identity is entirely out of the question, but the differences are such that if they actually were found in contemporary specimens, many prominent Lepidopterists, including Mr. Ch. Oberthür himself, would treat these differences as being of "specific" value. In fact, Clerck's figure of *Papilio deiphobus* resembles much more that insect which Felder separated as a distinct species (*Papilio deiphontes*) than it does Oberthür's figure of a specimen of *deiphobus* caught in 1893. Oberthür must have been led by that kind of reasoning indicated in the above text, else he could not have spoken of a "proof" that the species in question have not undergone "the least modification." This kind of reasoning is: first the figures of Clerck are mentally corrected according to the characters of recent specimens, then the characters thus corrected are pronounced to be identical with those of recent specimens.

I by no means will say that the particular species in question have been transformed since Linné's time; but I maintain that if there is any evidence as to transformation or non-transformation, the evidence is certainly in favour of transformation.

[†] Kerner, *Gute und schlechte Arten*, gives many illustrations of the transformation of plants.

[‡] Darwin, *Variation of Animals and Plants under Domestication*, 2nd edition, London, 1888, p. 119.

[§] Weismann, *Studies in the Theory of Descent*. From pupae of the southern form of *Polyommatus phlaeas* brought from Italy to Germany imagines emerged which were intermediate between the Italian and German forms.

[‖] Scudder, *Butterflies of New England* II. 1889, p. 1175, gives a detailed account of the gradual spread of *Pieris rapae*, which butterfly was first noticed in Canada in 1860, and describes a new variety (*novangliae*) into which *rapae* has developed.

However, we are not entirely left without evidence that transformation is actually going on under our eyes. We know from many plants † and a small number of animals that geographical races, when reared under conditions other than those of the country where the race lives, change in characters; we refer to the Porto Santo rabbits,‡ and *Polyommatus phlaeas*,§ and *Pieris brassicae*.‖ And a striking illustration of the fact that in a certain district a transformation of a species takes place has been published during recent years from different sides. A moth of the family *Geometridae*, *Amphidasis betularius*, has a black and a white form (with intergradations): the black form (*doubledayarius*), which for a long time was known to occur in Great Britain, was very rarely found in North-Western Germany; during the last ten to twenty years, however, the black form has become more frequent, and is at the Lower Rhine now nearly as common as the white form. Without trying to give an explanation of this phenomenon, which speaks for itself, it is of interest to note that in countries with a rational cultivation of the soil the changes in the immediate neighbourhood of the animals are very varied: the disappearance of swamps, planting of new forests on barren hills, artificial watering of pasture land, and so on, will not only destroy many forms, and give opportunity for other forms coming into the district; but these changes will most probably also have a certain amount of influence on those animals and plants which remain residents, at least on those forms which, like butterflies and plants, are very sensible to a change in the biological factors: and it would be highly interesting to have correct data whether perhaps a visible transformation of some animals and plants would be effected in a shorter time in a country with an intensive cultivation of the soil (like France) than in a country (like England) in which agriculture is more stagnant. Certainly we will not maintain that all the forms of animated nature have changed during the last hundred and fifty years, but will only draw attention to the historical side of the question, which cannot be entirely neglected. Palaeontology teaches us that there are forms which for a very long time have not changed, at least not in those parts which have been preserved; while, on the other hand, we know from palaeontology that in most cases a change must have taken place.

---

* Since the above was written I have received Oberthür's *Études d'Entomologie* XX. 1896. Here Oberthür tries to demonstrate from copies of old figures of *Lepidoptera* and figures of recently caught specimens that no change has taken place in these insects since Linné's time. The differences, however, which are exhibited by these old drawings and the figures of the recent specimens are not only so conspicuous that identity is entirely out of the question, but the differences are such that if they actually were found in contemporary specimens, many prominent Lepidopterists, including Mr. Ch. Oberthür himself, would treat these differences as being of "specific" value. In fact, Clerck's figure of *Papilio deiphobus* resembles much more that insect which Felder separated as a distinct species (*Papilio deiphontes*) than it does Oberthür's figure of a specimen of *deiphobus* caught in 1893. Oberthür must have been led by that kind of reasoning indicated in the above text, else he could not have spoken of a "proof" that the species in question have not undergone "the least modification." This kind of reasoning is: first the figures of Clerck are mentally corrected according to the characters of recent specimens, then the characters thus corrected are pronounced to be identical with those of recent specimens.

I by no means will say that the particular species in question have been transformed since Linné's time; but I maintain that if there is any evidence as to transformation or non-transformation, the evidence is certainly in favour of transformation.

† Kerner, *Gute und schlechte Arten*, gives many illustrations of the transformation of plants.

‡ Darwin, *Variation of Animals and Plants under Domestication*, 2nd edition, London, 1888, p. 119.

§ Weismann, *Studies in the Theory of Descent*. From pupae of the southern form of *Polyommatus phlaeas* brought from Italy to Germany imagines emerged which were intermediate between the Italian and German forms.

‖ Scudder, *Butterflies of New England* II. 1889. p. 1175, gives a detailed account of the gradual spread of *Pieris rapae*, which butterfly was first noticed in Canada in 1860, and describes a new variety (*novangliae*) into which *rapae* has developed.

At subsequent geological epochs the earth has been inhabited by different faunas and floras; that we know. If we had now before us all the specimens of animals and plants which ever have existed, and tried to group them as we do with the specimens in our collections, what would be the result? The gaps between the various forms would all be filled up by intergradations;* the Gorilla would be as different from the Giraffe as he is now; but tracing both animals back to their common ancestral form, we could draw up a series of individuals which would perfectly connect the two animals, and which would not allow us to draw a line of division: Gorilla and Giraffe thus would appear to be merely the extremes of the series. If, as we mostly practically do, the "species" are based only upon morphological differences, all the animals and plants would belong to one variable species. Any definition, therefore, based solely upon morphological differences must necessarily be a failure, and it follows also that the allegation that a certain form is a "distinct species" because there are no intergradations between it and the allied forms is in discordance with the theory of evolution, according to which the intergradations did occur, but are perhaps now extinct.

If we trace the line of ancestrals of two given types back to the form from which both have descended, we have for each type a separate line until we come to the primordial type in which both lines combine. The line of ancestors of every species comprises the different steps of development from the primordial form down to the recent form, and represents the historical polymorphism of the species, in opposition to contemporary polymorphism. Are the differences between the steps of development "specific" differences? *Hipparion* and *Equus*, though assumed to stand in illustration of the fact that in a certain district a transformation of a species takes place has been published during recent years from different sides. A moth of the family *Geometridae*, *Amphidasis betularius*, has a black and a white form (with intergradations): the black form (*doubledayarius*), which for a long time was known to occur in Great Britain, was very rarely found in North-Western Germany; during the last ten to twenty years, however, the black form has become more frequent, and is at the Lower Rhine now nearly as common as the white form. Without trying to give an explanation of this phenomenon, which speaks for itself, it is of interest to note that in countries with a rational cultivation of the soil the changes in the immediate neighbourhood of the animals are very varied: the disappearance of swamps, planting of new forests on barren hills, artificial watering of pasture land, and so on, will not only destroy many forms, and give opportunity for other forms coming into the district; but these changes will most probably also have a certain amount of influence on those animals and plants which remain residents, at least on those forms which, like butterflies and plants, are very sensible to a change in the biological factors: and it would be highly interesting to have correct data whether perhaps a visible transformation of some animals and plants would be effected in a shorter time in a country with an intensive cultivation of the soil (like France) than in a country (like England) in which agriculture is more stagnant. Certainly we will not maintain that all the forms of animated nature have changed during the last hundred and fifty years, but will only draw attention to the historical side of the question, which cannot be entirely neglected. Palaeontology teaches us that there are forms which for a very long time have not changed, at least not in those parts which have been preserved; while, on the other hand, we know from palaeontology that in most cases a change must have taken place.

---

* Romanes, *Darwin and After Darwin* II. London. 1895. p. 282.

At subsequent geological epochs the earth has been inhabited by different faunas and floras; that we know. If we had now before us all the specimens of animals and plants which ever have existed, and tried to group them as we do with the specimens in our collections, what would be the result? The gaps between the various forms would all be filled up by intergradations;* the Gorilla would be as different from the Giraffe as he is now; but tracing both animals back to their common ancestral form, we could draw up a series of individuals which would perfectly connect the two animals, and which would not allow us to draw a line of division: Gorilla and Giraffe thus would appear to be merely the extremes of the series. If, as we mostly practically do, the "species" are based only upon morphological differences, all the animals and plants would belong to one variable species. Any definition, therefore, based solely upon morphological differences must necessarily be a failure, and it follows also that the allegation that a certain form is a "distinct species" because there are no intergradations between it and the allied forms is in discordance with the theory of evolution, according to which the intergradations did occur, but are perhaps now extinct.

If we trace the line of ancestrals of two given types back to the form from which both have descended, we have for each type a separate line until we come to the primordial type in which both lines combine. The line of ancestors of every species comprises the different steps of development from the primordial form down to the recent form, and represents the historical polymorphism of the species, in opposition to contemporary polymorphism. Are the differences between the steps of development "specific" differences? *Hipparion* and *Equus*, though assumed to stand in the relationship of ancestor and descendant, are treated as members of different families; if it is right to keep ancestor and descendant, in spite of the intergradations which have existed according to the theory of evolution, in separate families in this case, why do we not do it in the case of the horses which our forefathers rode and those which live now? If it is the presence of morphological difference which leads us to split up in the one case, and the absence of such difference in the other case to unite, why then are *Distomum*, *Redia*, and *Cercaria*; *Rhabdonema* and *Rhabditis*; *Vanessa levana* and its offspring *prorsa*, the same species? Morphological difference alone is not a criterion of specific distinctness.

---

* Romanes, *Darwin and After Darwin* II. London, 1895. p. 282.

Besides the morphological differences among animals we observe a mental or psychological difference. It has often been noticed that in mixed flocks of sheep* or cattle the individuals belonging to the same race often keep separate from the rest, and it is also well known that in the state of nature strangers are driven away or even killed. Though psychological selection, as manifested in these cases, is of importance to accelerate the transformation of a variety and to fix the varietal characters, we believe that among domesticated animals it is very often not racial community that keeps the individuals together, but the circumstance of being accustomed to one another. In some districts of Germany all the geese of a village are driven to pasture in one large flock; when on the pasture ground, the individuals belonging to each house keep together, even if they are not the offspring of the same parents, but are brought together from different villages as goslings: this keeping together is an expression not of community of characters, nor of community of descent, but of community of the stable.

For us systematists that kind of psychological variation is of more interest which is the immediate outcome of morphological differences in the organs of sense and in the organs which are destined to affect the senses. The variability of the organs of sense among higher animals, and the difference of discriminating power among the individuals of the same species and race, are facts so well known that it is sufficient to remind the reader of the variability in the eyesight of men, or of the difference between dogs in regard to the power of smell. Among lower animals the senses are often very differently developed in the various families; in insects the power of discriminating form and colour seems generally to be rather weak, while in some families the organ of smell is highly developed. Carrion- and dung-beetles are able not only to smell the carrion or dung from a great distance, but, what is more important, they distinguish between the scent of carrion and that of dung. The sexes of *Lepidoptera* and *Coleoptera* are brought together by differences in the scent of the sexual scent-glands of the various forms; *females* of certain moths attract great numbers of *males*, even if the *female* is kept in a box with holes, and there is not the least doubt that the *males* of the various species of a genus follow the scent of the respective *females* and not that of allied species. As individuals of one species sometimes come to a *female* of another species, and as, further, dung-beetles are occasionally attracted by carrion, we must conclude that the specimens of dung-beetles really perceive the scent of dung *and* carrion, and that the *males* of insects not only perceive the scent of the *females* of their own species, but also that of other species. The phenomenon that dung-beetles come to dung, and that the *males* of a given species of insect follow the scent of the *females* of their species, cannot be explained by the assumption that the organ of smell of the specimens is so constructed that the insect is not able to perceive any scent but that particular one. The specimens of allied species, therefore, the relationship of ancestor and descendant, are treated as members of different families; if it is right to keep ancestor and descendant, in spite of the intergradations which have existed according to the theory of evolution, in separate families in this case, why do we not do it in the case of the horses which our forefathers rode and those which live now? If it is the presence of morphological difference which leads us to split up in the one case, and the absence of such difference in the other case to unite, why then are *Distomum*, *Redia*, and *Cercaria*; *Rhabdonema* and *Rhabditis*; *Vanessa levana* and its offspring *prorsa*, the same species? Morphological difference alone is not a criterion of specific distinctness.

---

* Darwin, *Variation of Animals*, etc., 2nd Ed. London, 1888, p. 145.

Besides the morphological differences among animals we observe a mental or psychological difference. It has often been noticed that in mixed flocks of sheep* or cattle the individuals belonging to the same race often keep separate from the rest, and it is also well known that in the state of nature strangers are driven away or even killed. Though psychological selection, as manifested in these cases, is of importance to accelerate the transformation of a variety and to fix the varietal characters, we believe that among domesticated animals it is very often not racial community that keeps the individuals together, but the circumstance of being accustomed to one another. In some districts of Germany all the geese of a village are driven to pasture in one large flock; when on the pasture ground, the individuals belonging to each house keep together, even if they are not the offspring of the same parents, but are brought together from different villages as goslings: this keeping together is an expression not of community of characters, nor of community of descent, but of community of the stable.

For us systematists that kind of psychological variation is of more interest which is the immediate outcome of morphological differences in the organs of sense and in the organs which are destined to affect the senses. The variability of the organs of sense among higher animals, and the difference of discriminating power among the individuals of the same species and race, are facts so well known that it is sufficient to remind the reader of the variability in the eyesight of men, or of the difference between dogs in regard to the power of smell. Among lower animals the senses are often very differently developed in the various families; in insects the power of discriminating form and colour seems generally to be rather weak, while in some families the organ of smell is highly developed. Carrion- and dung-beetles are able not only to smell the carrion or dung from a great distance, but, what is more important, they distinguish between the scent of carrion and that of dung. The sexes of *Lepidoptera* and *Coleoptera* are brought together by differences in the scent of the sexual scent-glands of the various forms; *females* of certain moths attract great numbers of *males*, even if the *female* is kept in a box with holes, and there is not the least doubt that the *males* of the various species of a genus follow the scent of the respective *females* and not that of allied species. As individuals of one species sometimes come to a *female* of another species, and as, further, dung-beetles are occasionally attracted by carrion, we must conclude that the specimens of dung-beetles really perceive the scent of dung *and* carrion, and that the *males* of insects not only perceive the scent of the *females* of their own species, but also that of other species. The phenomenon that dung-beetles come to dung, and that the *males* of a given species of insect follow the scent of the *females* of their species, cannot be explained by the assumption that the organ of smell of the specimens is so constructed that the insect is not able to perceive any scent but that particular one. The specimens of allied species, therefore, discriminate between the various scents, and follow that scent which, to put it more personally, incites them most. We have here a psychological selection. Now, if a variation takes place in the organ of smell and in the scent-producing glands, it seems to us evident that the effect will be such that the varietal individuals do not follow the same scent as that to which the normal specimens give preference, but select a varietal scent. Careful observations about psychological variation are extremely scarce; but we can give a beautiful illustration on the authority of Professor Standfuss,* who says that at Zürich *males* of *Callimorpha dominula* came very rarely to *females* of the Italian variety *persona*, while they were attracted in great numbers by the *females* of *dominula*. We see here that morphological and psychological variation can go hand in hand. If the power of discriminating scent is so highly developed throughout the order of *Lepidoptera* as in the case of *Callimorpha dominula*, we have a ready explanation of the phenomenon that the scent-organs, compared with the colour and pattern of the wings, are so constant in *Lepidoptera*. It is readily conceivable that the relative constancy of the scent-organs of *Lepidoptera* is a consequence of psychological selection based upon the difference in the organ of smell and in the scent-glands. And if we must admit the probability of the influence of this kind of mental selection, we are justified in concluding that psychological selection takes place in all animals which have one or the other organ of sense highly developed. As, however, with the various organs of sense only certain kinds of characters are perceivable, it is obvious that in different groups of animals psychological selection will affect different sets of characters according to which organ of sense has a high power of discrimination. Thus it seems to us intelligible that there exists such a strong contrast between *Lepidoptera* and birds in respect to the constancy of colour and markings. The great variability in colour in the order of *Lepidoptera* and the relatively slight variability † in scent-organs can be accounted for by the presence of selection as to scent-organs and the absence of selection as to colour,‡ while the surprisingly great constancy even in the shade of colour among birds may largely be due to the sharp eyesight of these animals rendering them capable of distinguishing between shades of colour, and hence inducing them to associate with specimens of their own colour and to drive differently coloured individuals away.

---

* Darwin, *Variation of Animals*, etc., 2nd Ed. London, 1888, p. 145.

The effect of the variation of psychical qualities as dependent on the variability of the organs of sense can, like the variation of morphological characters, be classified in individual, geographical, and historical polymorphism. The consideradiscriminate between the various scents, and follow that scent which, to put it more personally, incites them most. We have here a psychological selection. Now, if a variation takes place in the organ of smell and in the scent-producing glands, it seems to us evident that the effect will be such that the varietal individuals do not follow the same scent as that to which the normal specimens give preference, but select a varietal scent. Careful observations about psychological variation are extremely scarce; but we can give a beautiful illustration on the authority of Professor Standfuss,[*] who says that at Zürich *males* of *Callimorpha dominula* came very rarely to *females* of the Italian variety *persona*, while they were attracted in great numbers by the *females* of *dominula*. We see here that morphological and psychological variation can go hand in hand. If the power of discriminating scent is so highly developed throughout the order of *Lepidoptera* as in the case of *Callimorpha dominula*, we have a ready explanation of the phenomenon that the scent-organs, compared with the colour and pattern of the wings, are so constant in *Lepidoptera*. It is readily conceivable that the relative constancy of the scent-organs of *Lepidoptera* is a consequence of psychological selection based upon the difference in the organ of smell and in the scent-glands. And if we must admit the probability of the influence of this kind of mental selection, we are justified in concluding that psychological selection takes place in all animals which have one or the other organ of sense highly developed. As, however, with the various organs of sense only certain kinds of characters are perceivable, it is obvious that in different groups of animals psychological selection will affect different sets of characters according to which organ of sense has a high power of discrimination. Thus it seems to us intelligible that there exists such a strong contrast between *Lepidoptera* and birds in respect to the constancy of colour and markings. The great variability in colour in the order of *Lepidoptera* and the relatively slight variability[†] in scent-organs can be accounted for by the presence of selection as to scent-organs and the absence of selection as to colour,[‡] while the surprisingly great constancy even in the shade of colour among birds may largely be due to the sharp eyesight of these animals rendering them capable of distinguishing between shades of colour, and hence inducing them to associate with specimens of their own colour and to drive differently coloured individuals away.

---

* Standfuss, *Handbuch für Schmetterlingssammler*. Jena. 1896. p. 107.

† The scent-organs of *Lepidoptera*, especially those of the *males*, are not constant in every case: there are even species in which they are very variable; and the colour of birds is also not constant in every species.

‡ Eimer, *Artbildung und Verwandtschaft bei Schmetterlingen*, tries to "prove" on the ground of his studies on the wing-pattern of Papilios that the transmutation of animated nature takes place without natural selection. But even if this be true as regards a direct effect of selection on the wing-pattern, it is conceivable that psychological selection, which is a part of natural selection, can have, besides the direct influence on "structural" characters, an indirect influence on the distribution of colour on the wings. Eimer is in so far quite right as he says with Darwin (not against Darwin) that incipient varieties cannot have been originated by natural selection; where a "selection" takes place, there must already be a difference amongst the individuals. As Eimer expressly says that natural selection cannot produce species but only preserve species, and as, further, Eimer actually does not show how species (conforming to Eimer's definition of species) but only how varieties originate, I cannot perceive why we should not attribute to natural selection the preservation of *varietal* characters. Variation is, according to Darwin, not the outcome of natural selection, but is the premiss of natural selection; varietal characters can be preserved by selection and increased by survival of the fittest. I do not perceive any great contrast between Darwin and Eimer in respect to these points.

The effect of the variation of psychical qualities as dependent on the variability of the organs of sense can, like the variation of morphological characters, be classified in individual, geographical, and historical polymorphism. The consideration of these three kinds of polymorphism in the previous lines led us to the conclusion that morphological differences of any kind and degree are not decisive criteria as to specific distinctness; the systematist actually sinks his species in spite of distinguishing characters as soon as it is proved that the morphologically different forms appear among the offspring of the same *female*. The most general case of bodily difference which is not regarded as being specific is the difference between *males* and *females*; notwithstanding the great dissimilarity which the sexes so often exhibit, not only in the reproductive organs, but also in other morphological characters, the systematist puts *male* and *female* together in one species, and hence makes at once the concession that his term "species" is not a purely morphological one, but that the higher criterion of the term is of a physiological kind.

---

[*] Standfuss, *Handbuch für Schmetterlingssammler*. Jena. 1896. p. 107.

[†] The scent-organs of *Lepidoptera*, especially those of the *males*, are not constant in every case: there are even species in which they are very variable; and the colour of birds is also not constant in every species.

[‡] Eimer, *Artbildung und Verwandtschaft bei Schmetterlingen*, tries to "prove" on the ground of his studies on the wing-pattern of Papilios that the transmutation of animated nature takes place without natural selection. But even if this be true as regards a direct effect of selection on the wing-pattern, it is conceivable that psychological selection, which is a part of natural selection, can have, besides the direct influence on "structural" characters, an indirect influence on the distribution of colour on the wings Eimer is in so far quite right as he says with Darwin (not against Darwin) that incipient varieties cannot have been originated by natural selection; where a "selection" takes place, there must already be a difference amongst the individuals. As Eimer expressly says that natural selection cannot produce species but only preserve species, and as, further, Eimer actually does not show how species (conforming to Eimer's definition of species) but only how varieties originate, I cannot perceive why we should not attribute to natural selection the preservation of *varietal* characters. Variation is, according to Darwin, not the outcome of natural selection, but is the premiss of natural selection; varietal characters can be preserved by selection and increased by survival of the fittest. I do not perceive any great contrast between Darwin and Eimer in respect to these points.

Although morphological identity means also specific identity, the inverse that specific identity means morphological identity is not correct. The question, therefore, is now, which physiological divergence we will take as the real criterion of specific distinctness.

We have seen above that the line of ancestors of a given type can be divided into a recent portion which is independent of the lines of ancestors of all other types, and into a remote portion in which the lines of several types are combined. The specific difference which now keeps allied types separate was absent from them in remote times; what now is specifically different was formerly specifically identical. Hence a definition of "species," *i.e.* a definition of what makes two types specifically different, has to exclude any relation to the ancestral forms of the given types, but has to take into consideration the contemporary types and their descendants. For the sake of argument let us assume all types of animals and plants were monogamic, so that every individual would produce offspring without copulation with another individual. The question as to the characters of the descendants would be twofold: first, the descendants of a type (taken as a whole) become under certain conditions so changed that the gap which separates them from the descendants of another type is entirely filled up by intergradations, or that the descendants of both types entirely fuse together in characters; or, second, the sum of the descendants of each type remains under all conditions separated by a morphological gap from all other sums of descendants, whether the characters change or not. We have already referred to the transplantation of plants and animals by which it has been proved that forms which were unhesitatingly considered specifically different became identical. The divergency in the development of forms has in these cases been annihilated, and we must conclude that similar divergencies will in nature also be annihilated when the necessary conditions arise. If, therefore, *all* the various types in animated nature were different only to that degree, it follows that under favourable circumstances all these different forms would fuse together to one single type. Divergency would change into convergency and identity, and there would be no question as to species. As we, however, observe that fusing together is restricted to the nearest allied types, and that with the greater divergency of allied forms the possibility of fusing decreases until the forms remain separate under any condition, the term "species" as an expression of the divergency in nature must be an expression of that divergency which, though starting from identity in the ancestral forms, will never again develop into identity.

In the case of sexual propagation the question is more intricate in consequence of the intercrossing which takes place between different types. The question as to the lines of descendants is threefold: the line of descendants of a given type fuses tion of these three kinds of polymorphism in the previous lines led us to the conclusion that morphological differences of any kind and degree are not decisive criteria as to specific distinctness; the systematist actually sinks his species in spite of distinguishing characters as soon as it is proved that the morphologically different forms appear among the offspring of the same *female*. The most general case of bodily difference which is not regarded as being specific is the difference between *males* and *females*; notwithstanding the great dissimilarity which the sexes so often exhibit, not only in the reproductive organs, but also in other morphological characters, the systematist puts *male* and *female* together in one species, and hence makes at once the concession that his term "species" is not a purely morphological one, but that the higher criterion of the term is of a physiological kind.

Although morphological identity means also specific identity, the inverse that specific identity means morphological identity is not correct. The question, therefore, is now, which physiological divergence we will take as the real criterion of specific distinctness.

We have seen above that the line of ancestors of a given type can be divided into a recent portion which is independent of the lines of ancestors of all other types, and into a remote portion in which the lines of several types are combined. The specific difference which now keeps allied types separate was absent from them in remote times; what now is specifically different was formerly specifically identical. Hence a definition of "species," *i.e.* a definition of what makes two types specifically different, has to exclude any relation to the ancestral forms of the given types, but has to take into consideration the contemporary types and their descendants. For the sake of argument let us assume all types of animals and plants were monogamic, so that every individual would produce offspring without copulation with another individual. The question as to the characters of the descendants would be twofold: first, the descendants of a type (taken as a whole) become under certain conditions so changed that the gap which separates them from the descendants of another type is entirely filled up by intergradations, or that the descendants of both types entirely fuse together in characters; or, second, the sum of the descendants of each type remains under all conditions separated by a morphological gap from all other sums of descendants, whether the characters change or not. We have already referred to the transplantation of plants and animals by which it has been proved that forms which were unhesitatingly considered specifically different became identical. The divergency in the development of forms has in these cases been annihilated, and we must conclude that similar divergencies will in nature also be annihilated when the necessary conditions arise. If, therefore, *all* the various types in animated nature were different only to that degree, it follows that under favourable circumstances all these different forms would fuse together to one single type. Divergency would change into convergency and identity, and there would be no question as to species. As we, however, observe that fusing together is restricted to the nearest allied types, and that with the greater divergency of allied forms the possibility of fusing decreases until the forms remain separate under any condition, the term "species" as an expression of the divergency in nature must be an expression of that divergency which, though starting from identity in the ancestral forms, will never again develop into identity.

In the case of sexual propagation the question is more intricate in consequence of the intercrossing which takes place between different types. The question as to the lines of descendants is threefold: the line of descendants of a given type fuses completely together with that of one or more other types under certain conditions, and the descendants are qualified for propagation; secondly, the line of descendants remains separate under every condition; and thirdly, the lines of descendants are partly fused by the appearance of cross-products, which, however, are not fully qualified for propagation. The two first points are the same as those mentioned under monogamic propagation. The third case is of little consequence; the cross-products, though often obscuring the fact of the independence of the descendants of two given types, have really no influence upon the lines of descendants, as the offspring of the cross-products soon become extinct, and therefore do not affect the characters of those descendants of the present types which are not cross-products. In asexual and in sexual propagation we observe that the lines of descendants of the various types exhibit this contrast, that they are either capable of fusion or not capable of fusion: in the first case divergent development changes under certain conditions into convergent development, and ends in identity; in the second case the development ends under every condition in divergency.

In order to see clearly which kind of divergency in animated nature we shall have to term *specific*, we will shortly recapitulate those points which have to be taken into consideration.

1. The presence of morphological distinguishing characters is not a final criterion of specific distinctness; a definition of species based solely upon such differences not only would not take into account individual, geographical, and historical polymorphism, but would, if consequently applied, make every individual specifically distinct, as we have seen that the sum of the characters of every individual is different from the sum of the characters of every other individual.

2. Though according to the theory of evolution every species is the outcome of the transmutation of another, ancestral species, we have only morphological characters to distinguish ancestral and descendant species by. Therefore, considering what is said under 1, a final criterion whether the different types which form the direct line of ancestors of a given type are "specifically" different is wanting; palaeontology provides us with morphologically different specimens, which can never be proved to have been specifically distinct. And as, further, allied species have at a former period not been specifically different, a definition of the term "species" based upon evolution must leave the line of extinct ancestors altogether out of consideration.

3. As the theory of evolution further implies that a species can in the course of time develop into one or more descendant species, the term "species" rigorously applied must be restricted to contemporary individuals. Hence the definition of the term "species" as designating a certain kind, and always the same kind, of diversity throughout animated nature, has to be arrived at by comparing the divergency of coexistent types.

4. The theory of creation explains the diversity in animated nature by assuming that every species from the time of its special creation to its extinction is a unit separate from every other unit; allied species have never been and will never be the same. The theory of evolution, abandoning special creation of each species, puts in its place divergent development from a common form, but to explain the actually existing great discrepancy in nature must assume, like the theory of creation, that when a certain degree of divergency is attained the form of animal or plant exhibiting this divergency can never become one with any other form. This degree of divergency stands in the same contraposition to all lower degrees of

completely together with that of one or more other types under certain conditions, and the descendants are qualified for propagation; secondly, the line of descendants remains separate under every condition; and thirdly, the lines of descendants are partly fused by the appearance of cross-products, which, however, are not fully qualified for propagation. The two first points are the same as those mentioned under monogamic propagation. The third case is of little consequence; the cross-products, though often obscuring the fact of the independence of the descendants of two given types, have really no influence upon the lines of descendants, as the offspring of the cross-products soon become extinct, and therefore do not affect the characters of those descendants of the present types which are not cross-products. In asexual and in sexual propagation we observe that the lines of descendants of the various types exhibit this contrast, that they are either capable of fusion or not capable of fusion: in the first case divergent development changes under certain conditions into convergent development, and ends in identity; in the second case the development ends under every condition in divergency.

In order to see clearly which kind of divergency in animated nature we shall have to term *specific*, we will shortly recapitulate those points which have to be taken into consideration.

1. The presence of morphological distinguishing characters is not a final criterion of specific distinctness; a definition of species based solely upon such differences not only would not take into account individual, geographical, and historical polymorphism, but would, if consequently applied, make every individual specifically distinct, as we have seen that the sum of the characters of every individual is different from the sum of the characters of every other individual.

2. Though according to the theory of evolution every species is the outcome of the transmutation of another, ancestral species, we have only morphological characters to distinguish ancestral and descendant species by. Therefore, considering what is said under 1, a final criterion whether the different types which form the direct line of ancestors of a given type are "specifically" different is wanting; palaeontology provides us with morphologically different specimens, which can never be proved to have been specifically distinct. And as, further, allied species have at a former period not been specifically different, a definition of the term "species" based upon evolution must leave the line of extinct ancestors altogether out of consideration.

3. As the theory of evolution further implies that a species can in the course of time develop into one or more descendant species, the term "species" rigorously applied must be restricted to contemporary individuals. Hence the definition of the term "species" as designating a certain kind, and always the same kind, of diversity throughout animated nature, has to be arrived at by comparing the divergency of coexistent types.

4. The theory of creation explains the diversity in animated nature by assuming that every species from the time of its special creation to its extinction is a unit separate from every other unit; allied species have never been and will never be the same. The theory of evolution, abandoning special creation of each species, puts in its place divergent development from a common form, but to explain the actually existing great discrepancy in nature must assume, like the theory of creation, that when a certain degree of divergency is attained the form of animal or plant exhibiting this divergency can never become one with any other form. This degree of divergency stands in the same contraposition to all lower degrees of

development, which allow a fusion of the respective forms, as the negative does to the affirmative, and therefore is different from the lower degrees of development not only as to degree, but also as to kind.

5. From the fourth point it follows that if specific difference means a difference of kind, not only of degree, the chief criterion of specific distinctness of a given form of animal or plant is the impossibility of fusion with other forms.

Hence we have to accept the following definition of the term "species":—

A species is a group of individuals which is differentiated from all other contemporary groups by one or more characters, and of which the descendants which are fully qualified for propagation form again under all conditions of life one or more groups of individuals differentiated from the descendants of all other groups by one or more characters.

The reasons why we do not accept one of the definitions of species as given by other authors are best stated by shortly discussing the definitions of Eimer, Romanes, and Wallace.

I. Eimer's definition [*] is a purely physiological one:—

"Species are groups of individuals which are so modified that sexual intercourse does no longer take place between them and other groups, or that successful intercourse is not unlimitedly possible."

Apart from the criteria of the term "species" in this definition being negative, we cannot accept the definition simply because it is not a definition in consequence of its allowing us a *choice* between two different criteria. Let us discuss these criteria separately:—

1. "Species are groups of individuals which are so modified that sexual intercourse does no longer take place."

According to this definition the prevention of intercrossing is a consequence of the modification of the groups of individuals. From several sides attention has been drawn to the occurrence of psychological selection among the individuals of the same species, especially among specimens belonging to varieties of domesticated animals. As in these cases intercrossing does not take place on account of a dislike of the respective varieties, *i.e.* as the prevention of intercrossing is a consequence of the modification of a species into varieties, these varieties would conform to Eimer's definition, and therefore would have to be considered as distinct species.

2. "Species are groups of individuals which are so modified that successful sexual intercourse is not unlimitedly possible."

In the second part of his studies on Papilios [†] Eimer claims priority over Romanes as to the principal idea upon which Romanes based his theory of Physiological Selection. The chief premiss of this theory is the occurrence of such a variation among the individuals of the same species that a group of specimens does not only not cross with the rest of the individuals on account of dislike, but is infertile or restrictedly fertile with them, whereas the specimens of that group are *inter se* completely fertile. If such a physiological variation occurs, and there is no reason why it should not occur, that group of individuals would constitute a species according to Eimer's definition, in spite of the absence of morphological distinguishing characters, and in spite of the offspring of the physiological variety belonging partly to the development, which allow a fusion of the respective forms, as the negative does to the affirmative, and therefore is different from the lower degrees of development not only as to degree, but also as to kind.

---

[*] Eimer, *Artbildung und Verwandtschaft bei Schmetterlingen*, 1889, p. 16. Romanes, in ***Darwin and After Darwin***, 1895, p. 229, says that the "purely physiological definition is not nowadays entertained by any naturalist."

[†] Eimer, *Artbildung und Verwandtschaft bei Schmetterlingen* II. Jena, 1895, p. 14.

5. From the fourth point it follows that if specific difference means a difference of kind, not only of degree, the chief criterion of specific distinctness of a given form of animal or plant is the impossibility of fusion with other forms.

Hence we have to accept the following definition of the term "species":—

A species is a group of individuals which is differentiated from all other contemporary groups by one or more characters, and of which the descendants which are fully qualified for propagation form again under all conditions of life one or more groups of individuals differentiated from the descendants of all other groups by one or more characters.

The reasons why we do not accept one of the definitions of species as given by other authors are best stated by shortly discussing the definitions of Eimer, Romanes, and Wallace.

I. Eimer's definition * is a purely physiological one:—

"Species are groups of individuals which are so modified that sexual intercourse does no longer take place between them and other groups, or that successful intercourse is not unlimitedly possible."

Apart from the criteria of the term "species" in this definition being negative, we cannot accept the definition simply because it is not a definition in consequence of its allowing us a *choice* between two different criteria. Let us discuss these criteria separately:—

1. "Species are groups of individuals which are so modified that sexual intercourse does no longer take place."

According to this definition the prevention of intercrossing is a consequence of the modification of the groups of individuals. From several sides attention has been drawn to the occurrence of psychological selection among the individuals of the same species, especially among specimens belonging to varieties of domesticated animals. As in these cases intercrossing does not take place on account of a dislike of the respective varieties, *i.e.* as the prevention of intercrossing is a consequence of the modification of a species into varieties, these varieties would conform to Eimer's definition, and therefore would have to be considered as distinct species.

2. "Species are groups of individuals which are so modified that successful sexual intercourse is not unlimitedly possible."

In the second part of his studies on Papilios † Eimer claims priority over Romanes as to the principal idea upon which Romanes based his theory of Physiological Selection. The chief premiss of this theory is the occurrence of such a variation among the individuals of the same species that a group of specimens does not only not cross with the rest of the individuals on account of dislike, but is infertile or restrictedly fertile with them, whereas the specimens of that group are *inter se* completely fertile. If such a physiological variation occurs, and there is no reason why it should not occur, that group of individuals would constitute a species according to Eimer's definition, in spite of the absence of morphological distinguishing characters, and in spite of the offspring of the physiological variety belonging partly to the normal form of the species. Even if the physiological difference is accompanied by a morphological difference, the variety cannot be considered a species as long as some of its offspring are of the normal form ; *A* and *B* are not specifically distinct as long as *A* produces *B*, and *B* produces *A*.

---

* Eimer, *Artbildung und Verwandtschaft bei Schmetterlingen*, 1889, p. 16. Romanes, in *Darwin and After Darwin*, 1895, p. 229, says that the "purely physiological definition is not nowadays entertained by any naturalist."

† Eimer, *Artbildung und Verwandtschaft bei Schmetterlingen* II. Jena, 1895, p. 14.

II. Romanes's definition * is as follows :—

"A group of individuals which, however many characters they share with other individuals, agree in presenting one or more characters of a peculiar and hereditary kind, with some certain degree of distinctness."

This definition, if the words "and hereditary" were left out, would be based solely upon the presence of morphological difference. "Evolutionists," says Romanes, "have more and more grown to lay stress on the hereditary character of such peculiarities as they select for diagnostic features of specific distinctness. Indeed it is not too much to say that, at the present time, evolutionists in general recognise this character as, theoretically, indispensable to the constitution of a species." † Our objection against the word "hereditary," which does not "supply exactly that objective and rigid criterion of specific distinctness" which we necessarily require, is twofold :—

1. There are characters of an hereditary kind which are not specific. Indeed many of those peculiarities of individual varieties which regularly appear in every brood are hereditary, but do not make the individuals which exhibit them specifically distinct. Among the individuals of *Papilio sarpedon*,‡ to give an illustration, appear specimens (in New Britain regularly) which have one or two additional green spots on the forewing; in specimens from the Solomon Islands additional green spots are always present ; as for certain reasons we consider *Papilio sarpedon* to be the descendant of a species with a greater number of markings than *sarpedon* now has, the presence of such additional markings we have to explain by the assumption that these markings are inherited from the ancestors. We observe here restricted inheritance of a peculiar character in the individuals from various parts of the Indo-Australian regions, and constant inheritance of that character on the Solomon Islands. Notwithstanding that it is an hereditary character which distinguishes the respective individuals, these specimens are not specifically distinct from those individuals which are devoid of that character.

2. Specific characters are not unrestrictedly hereditary. It is a well-known fact that the various forms of some polymorphic species of butterflies are so distributed that the species is polymorphic in one, monomorphic in other districts. *Papilio aegeus* has a number of different *female*-forms in New Guinea, the Aru and Key Islands, while in Australia there is only one kind of *female*. *Papilio clytia* is remarkably dimorphic in India in both sexes—the varieties are called *clytia*-form and

---

* Romanes, *Darwin and After Darwin* II. 1895. p. 231.

† *Ibid.*

‡ In this article I have given the names of species and varieties without adding the "author" for two reasons. (1) The original meaning of a name has mostly changed, its application having become restricted or extended. The reference to the original author, therefore, would give us quite an erroneous idea about the extent in which the name is used in this article. Various writers apply the same name with the same original author to different forms of *Lepidoptera* ; hence it is necessary, in order to avoid confusion, to say precisely in which sense a name is here made use of. (2) As it is the contents of a name and not the name I have to deal with, the mere annexation of an author's name to the specific or varietal name would not convey to the reader any idea about the meaning of the name ; it is, therefore, necessary to give a reference to a book where the respective form has been figured or sufficiently described. Instead of giving the reference behind each name, I annex to this article, for the sake of simplicity, an alphabetical list of the species and varieties with the necessary references.

normal form of the species. Even if the physiological difference is accompanied by a morphological difference, the variety cannot be considered a species as long as some of its offspring are of the normal form ; *A* and *B* are not specifically distinct as long as *A* produces *B*, and *B* produces *A*.

II. Romanes's definition * is as follows :—

"A group of individuals which, however many characters they share with other individuals, agree in presenting one or more characters of a peculiar and hereditary kind, with some certain degree of distinctness."

This definition, if the words "and hereditary" were left out, would be based solely upon the presence of morphological difference. "Evolutionists," says Romanes, "have more and more grown to lay stress on the hereditary character of such peculiarities as they select for diagnostic features of specific distinctness. Indeed it is not too much to say that, at the present time, evolutionists in general recognise this character as, theoretically, indispensable to the constitution of a species." † Our objection against the word "hereditary," which does not "supply exactly that objective and rigid criterion of specific distinctness" which we necessarily require, is twofold :—

1. There are characters of an hereditary kind which are not specific. Indeed many of those peculiarities of individual varieties which regularly appear in every brood are hereditary, but do not make the individuals which exhibit them specifically distinct. Among the individuals of *Papilio sarpedon*,‡ to give an illustration, appear specimens (in New Britain regularly) which have one or two additional green spots on the forewing; in specimens from the Solomon Islands additional green spots are always present ; as for certain reasons we consider *Papilio sarpedon* to be the descendant of a species with a greater number of markings than *sarpedon* now has, the presence of such additional markings we have to explain by the assumption that these markings are inherited from the ancestors. We observe here restricted inheritance of a peculiar character in the individuals from various parts of the Indo-Australian regions, and constant inheritance of that character on the Solomon Islands. Notwithstanding that it is an hereditary character which distinguishes the respective individuals, these specimens are not specifically distinct from those individuals which are devoid of that character.

2. Specific characters are not unrestrictedly hereditary. It is a well-known fact that the various forms of some polymorphic species of butterflies are so distributed that the species is polymorphic in one, monomorphic in other districts. *Papilio aegeus* has a number of different *female*-forms in New Guinea, the Aru and Key Islands, while in Australia there is only one kind of *female*. *Papilio clytia* is remarkably dimorphic in India in both sexes—the varieties are called *clytia*-form and

---

* Romanes, *Darwin and After Darwin* II. 1895. p. 231.

† *Ibid.*

‡ In this article I have given the names of species and varieties without adding the "author" for two reasons. (1) The original meaning of a name has mostly changed, its application having become restricted or extended. The reference to the original author, therefore, would give us quite an erroneous idea about the extent in which the name is used in this article. Various writers apply the same name with the same original author to different forms of *Lepidoptera* ; hence it is necessary, in order to avoid confusion, to say precisely in which sense a name is here made use of. (2) As it is the contents of a name and not the name I have to deal with, the mere annexation of an author's name to the specific or varietal name would not convey to the reader any idea about the meaning of the name ; it is, therefore, necessary to give a reference to a book where the respective form has been figured or sufficiently described. Instead of giving the reference behind each name, I annex to this article, for the sake of simplicity, an alphabetical list of the species and varieties with the necessary references.

dissimilis-form—while on the Andaman Islands only a *dissimilis*-form and on the Philippines only a *clytia*-form occurs; both the Andaman and the Philippine monomorphic insects are not specifically distinct from the Indian dimorphic insect. The nearest ally of *Papilio clytia* is the very variable *Papilio paradoxus*.* If we assume that the Andaman and Philippine insects are the descendants of the Indian dimorphic *clytia*, or the latter the descendant of the former, or all three the descendants of a common ancestor, it is evident that the characters by which formerly (before the separation into three geographical races) the species was distinguished from *paradoxus* are not the same as those by which all forms from the three localities together (which forms now constitute the species) are at present distinguished from *paradoxus*.

We may add a few more illustrations from other well-known butterflies. The large Papuan butterflies usually called *Ornithoptera* are in the *male* sex of an orange, green, or blue colour. For the sake of argument let us assume that the green *priamus*, orange *croesus* and *lydius*, and blue *urvillianus* were derived from a common ancestor which had an orange *male*. The nearest ally is *O. tithonus*, which has a green *male*. In the diagnosis of the green ancestral forms of *tithonus* the difference in colour between it and the orange ally would have been a specific difference; the recent *tithonus* cannot be differentiated from *priamus* by the shade of colour, as both insects are green. This one specific character has not remained a specific character in *tithonus*, though perhaps the ancestral *tithonus* and the recent one are identical in colour, and though the character itself, therefore, has proved to be hereditary; on the other side, that one distinguishing character of the orange ancestor of *priamus*, *croesus*, *lydius*, and *urvillianus* has been inherited only by *lydius* and *croesus*, not by *priamus* and *urvillianus*, and therefore has proved to be only restrictedly hereditary.

One of the characters by which *Papilio eurypylus* is distinguished, for instance, from *P. sarpedon*, is the position and extent of the red costal mark on the underside of the hindwing. This mark is in *eurypylus* a small red spot before the costal nervure, while in *sarpedon* the spot is extended beyond the costal to the subcostal nervure. Quite recently Mr. Walter Rothschild received a series of specimens of *P. eurypylus* from the Kei Islands,† among which is one that has the red mark extended to the subcostal vein. The extent of this spot, which until now was a specific character of *eurypylus*, is no longer of specific value, and cannot serve to distinguish *eurypylus* from *sarpedon* or *macfarlanei*: in respect to the latter two species the form of the spot is hereditary, but no longer specific; in respect to *eurypylus* it is not unrestrictedly hereditary, and also no longer of specific value. Now, if it should happen that all specimens of *eurypylus* acquired the extended red mark and became at the same time in other characters still more different from *sarpedon* and *macfarlanei*, would then *eurypylus*, *sarpedon*, and *macfarlanei* of our days not be specifically different, because their offspring exhibited other distinguishing characters?

The objection against the use of the word "hereditary" in the definition of the term "species" which we have here raised is based immediately upon the assumption of the transmutation of species and their components (varieties). The species *A* and *B*, to put it figuratively, may have as specific characters *a* and *b* respectively; in the

---

* *Papilio echidna* from the lesser Sunda Islands is a *dissimilis*-form, but is perhaps specifically distinct; I do not take this insect into account here.

† Collected by Captain Cayley Webster. The importance of the record of individual aberrations is here again evident.

dissimilis-form—while on the Andaman Islands only a *dissimilis*-form and on the Philippines only a *clytia*-form occurs; both the Andaman and the Philippine monomorphic insects are not specifically distinct from the Indian dimorphic insect. The nearest ally of *Papilio clytia* is the very variable *Papilio paradoxus*.* If we assume that the Andaman and Philippine insects are the descendants of the Indian dimorphic *clytia*, or the latter the descendant of the former, or all three the descendants of a common ancestor, it is evident that the characters by which formerly (before the separation into three geographical races) the species was distinguished from *paradoxus* are not the same as those by which all forms from the three localities together (which forms now constitute the species) are at present distinguished from *paradoxus*.

We may add a few more illustrations from other well-known butterflies. The large Papuan butterflies usually called *Ornithoptera* are in the *male* sex of an orange, green, or blue colour. For the sake of argument let us assume that the green *priamus*, orange *croesus* and *lydius*, and blue *urvillianus* were derived from a common ancestor which had an orange *male*. The nearest ally is *O. tithonus*, which has a green *male*. In the diagnosis of the green ancestral forms of *tithonus* the difference in colour between it and the orange ally would have been a specific difference; the recent *tithonus* cannot be differentiated from *priamus* by the shade of colour, as both insects are green. This one specific character has not remained a specific character in *tithonus*, though perhaps the ancestral *tithonus* and the recent one are identical in colour, and though the character itself, therefore, has proved to be hereditary; on the other side, that one distinguishing character of the orange ancestor of *priamus*, *croesus*, *lydius*, and *urvillianus* has been inherited only by *lydius* and *croesus*, not by *priamus* and *urvillianus*, and therefore has proved to be only restrictedly hereditary.

One of the characters by which *Papilio eurypylus* is distinguished, for instance, from *P. sarpedon*, is the position and extent of the red costal mark on the underside of the hindwing. This mark is in *eurypylus* a small red spot before the costal nervure, while in *sarpedon* the spot is extended beyond the costal to the subcostal nervure. Quite recently Mr. Walter Rothschild received a series of specimens of *P. eurypylus* from the Kei Islands,† among which is one that has the red mark extended to the subcostal vein. The extent of this spot, which until now was a specific character of *eurypylus*, is no longer of specific value, and cannot serve to distinguish *eurypylus* from *sarpedon* or *macfarlanei*: in respect to the latter two species the form of the spot is hereditary, but no longer specific; in respect to *eurypylus* it is not unrestrictedly hereditary, and also no longer of specific value. Now, if it should happen that all specimens of *eurypylus* acquired the extended red mark and became at the same time in other characters still more different from *sarpedon* and *macfarlanei*, would then *eurypylus*, *sarpedon*, and *macfarlanei* of our days not be specifically different, because their offspring exhibited other distinguishing characters?

The objection against the use of the word "hereditary" in the definition of the term "species" which we have here raised is based immediately upon the assumption of the transmutation of species and their components (varieties). The species A and B, to put it figuratively, may have as specific characters a and b respectively; in the course of time, which need not be long, the species A and B develop into A^1 and B^1, with the characters a^1 and b^1 respectively; this change in characters may perhaps be due to the respective areas occupied by the species being suddenly extended or restricted. The characters a and b are, therefore, not inherited by A^1 and B^1; but A and B (and A^1 and B^1) are nevertheless specifically distinct.

---

* *Papilio echidna* from the lesser Sunda Islands is a *dissimilis*-form, but is perhaps specifically distinct; I do not take this insect into account here.

† Collected by Captain Cayley Webster. The importance of the record of individual aberrations is here again evident.

III. Wallace's definition of the term "species"* is a combination of definitions I. and II., with the addition that the specific characters are of an *adaptive* kind. As the objections raised under I. and II. apply also to Wallace's definition, we can restrict our remarks to a short discussion of that latter point. As a species is not only opposed to every other species, but is also to be distinguished from variety, the definition of the term "species" must be a guide for the distinction of species from variety. The kind of characters, therefore, to be mentioned in the definition must exclusively be distinctive of species; a certain quality alleged to be required to make a group of individuals specifically distinct must not be a quality that distinguishes variety from variety. The question is, therefore, are there varieties (as opposed to species) the distinguishing characters of which are adaptive? The theory of Natural Selection, so much supported by Wallace, gives an affirmative answer. All the varieties which are selected as the fittest are varieties with special adaptive characters. If we accept Natural Selection as a factor in evolution, we have consequently to concede that both species and varieties are "adapted to slightly different conditions of life." Hence it is evident that Wallace's definition of the term "species" includes a quality which is not exclusively specific, but applies also to the term "variety," and that we have to cancel altogether the restriction that specific characters are of an adaptive kind.

The principal objection here raised against those three definitions, which may be taken as fairly representing the various views of modern authors, is that the definitions, even when accepted as giving the general distinction between any two species, do not furnish us with a general criterion between species and varieties. This sounds baroque, but is a fact. There are varieties (as opposed to "species") which do no longer have sexual intercourse with the other individuals of the same species, and we must also assume that sometimes such an intercourse is not possible; there are varieties which exhibit hereditary distinguishing characters; and there are also varieties with adaptive distinguishing characters. The consequence of accepting a definition of the term "species" which does not exclude every kind of variety (*varietas* as opposed to *species*) leads naturally to the conclusion that there is no real distinction between "species" and "variety," and that it is purely conventional whether we call a form species or variety, an opinion by no means rarely met with even amongst us species-makers. For example, Butler says: † "For some years past I have held the view that what is generally understood by the term "species" (that is to say, a well-defined, distinct, and constant type, having no near allies) is non-existent in *Lepidoptera*, and that the nearest approach to it in this order is a constant, though but slightly differing, race or local form—that genera, in fact, consist wholly of a gradational series of such forms."

According to our definition there is, however, a real distinction between the course of time, which need not be long, the species A and B develop into A^1 and B^1, with the characters a^1 and b^1 respectively; this change in characters may perhaps be due to the respective areas occupied by the species being suddenly extended or restricted. The characters a and b are, therefore, not inherited by A^1 and B^1; but A and B (and A^1 and B^1) are nevertheless specifically distinct.

---

* *Darwinism* 1889. p. 167.

† *Ann. Mag. N. H.* (5). XIX. p. 103. It is easily perceivable from Dr. Butler's work on *Lepidoptera*, for instance from his revision of a group of butterflies called *Euploeinae*, that what Butler regards above as "species" is subspecies or geographical variety, the gradational series of which constitute the "species," and that his "genus" is the species.

III. Wallace's definition of the term "species"* is a combination of definitions I. and II., with the addition that the specific characters are of an *adaptive* kind. As the objections raised under I. and II. apply also to Wallace's definition, we can restrict our remarks to a short discussion of that latter point. As a species is not only opposed to every other species, but is also to be distinguished from variety, the definition of the term "species" must be a guide for the distinction of species from variety. The kind of characters, therefore, to be mentioned in the definition must exclusively be distinctive of species; a certain quality alleged to be required to make a group of individuals specifically distinct must not be a quality that distinguishes variety from variety. The question is, therefore, are there varieties (as opposed to species) the distinguishing characters of which are adaptive? The theory of Natural Selection, so much supported by Wallace, gives an affirmative answer. All the varieties which are selected as the fittest are varieties with special adaptive characters. If we accept Natural Selection as a factor in evolution, we have consequently to concede that both species and varieties are "adapted to slightly different conditions of life." Hence it is evident that Wallace's definition of the term "species" includes a quality which is not exclusively specific, but applies also to the term "variety," and that we have to cancel altogether the restriction that specific characters are of an adaptive kind.

The principal objection here raised against those three definitions, which may be taken as fairly representing the various views of modern authors, is that the definitions, even when accepted as giving the general distinction between any two species, do not furnish us with a general criterion between species and varieties. This sounds baroque, but is a fact. There are varieties (as opposed to "species") which do no longer have sexual intercourse with the other individuals of the same species, and we must also assume that sometimes such an intercourse is not possible; there are varieties which exhibit hereditary distinguishing characters; and there are also varieties with adaptive distinguishing characters. The consequence of accepting a definition of the term "species" which does not exclude every kind of variety (*varietas* as opposed to *species*) leads naturally to the conclusion that there is no real distinction between "species" and "variety," and that it is purely conventional whether we call a form species or variety, an opinion by no means rarely met with even amongst us species-makers. For example, Butler says: † "For some years past I have held the view that what is generally understood by the term "species" (that is to say, a well-defined, distinct, and constant type, having no near allies) is non-existent in *Lepidoptera*, and that the nearest approach to it in this order is a constant, though but slightly differing, race or local form—that genera, in fact, consist wholly of a gradational series of such forms."

According to our definition there is, however, a real distinction between the terms "species" and "variety," a distinction which indeed everybody silently accepts who considers the enormous numbers of different forms of animals and plants to be the outcome of divergent development, and expresses this development by the conventional figurative tree. If the specimens represented by any given portion of a branch of this tree were so constructed that under favourable circumstances they would be identical with the specimens represented by a portion of another branch, *i.e.* if any two branches could, and can, long after the common origin, merge together, then branch off again, merge together again, and so on, it would be preposterous to assume that this should never have happened. But if we thus should have to concede the possibility that the lines of ancestors of any two forms of plants or animals, say of the lion and the giraffe, were such that they first became widely divergent, then identical, then again widely divergent, not only the figurative tree, but also the kind of evolution it is meant to illustrate, would be pure nonsense. Therefore we take it that we are actually agreed upon that part of our definition which says that from a certain point a branch of the tree *cannot* merge together again with any other branch ; now, if we call every form which has reached this degree of development *specifically* distinct, we have an absolute distinction between species and the lower degrees of development.

---

* *Darwinism* 1889. p. 167.

† *Ann. Mag. N. H.* (5). XIX. p. 103. It is easily perceivable from Dr. Butler's work on *Lepidoptera*, for instance from his revision of a group of butterflies called *Euploeinae*, that what Butler regards above as "species" is subspecies or geographical variety, the gradational series of which constitute the "species," and that his "genus" is the species.

The question of specific distinctness or non-distinctness is therefore twofold : first one of morphological, and second one of physiological difference. As the systematist is practically not able to test by experiment the presence of the second distinction, it is obvious that he never can *prove* with *certainty* from the specimens alone whether the distinguishing morphological characters they exhibit are of specific value or not. However, we are able to arrive at a probably correct conclusion without testing in each case the specific distinctness, if we take into account the way in which divarication of species comes about, and if we further compare the characters of such forms as have been tested to be specifically distinct.

For our present purposes it is quite irrelevant whether the causes of the transmutation and divarication of species are those factors which are maintained by the Neo-Darwinians to be the sole agents, or those which the Neo-Lamarckians consider to be alone effective. Hence we shall abstain from any discussion of the much contested final causes of divergent development, and shall simply ask, which is the way that leads from variability of a species to divarication of this species into more species? Our purpose allows us to simplify the question still more and to restrict the discussion to the two points: first, can a species develop into two (or more) species without isolation? secondly, can isolation as such transmute one species into two (or more)?

The most extreme kind of variability of a species logically possible is that in which the varieties composing the species are not only morphologically but also physiologically different. As upon the occurrence of such variation Romanes's theory of Physiological Selection, which we have had to allude to several times, is founded, we may be allowed to annex our notes to a short discussion of this theory as far as it bears upon our particular question.

In order to explain the infertility or restricted fertility between different species Romanes assumes that the divarication of one species into more species has something to do with the occurrence of such a variation that some individuals of a given species are not fertile with the rest of the species, but are fully fertile *inter se.* That variety, though living in the same district as the normal form of the species, will develop divergently, according to the theory, and give rise to a new species, as it terms "species" and "variety," a distinction which indeed everybody silently accepts who considers the enormous numbers of different forms of animals and plants to be the outcome of divergent development, and expresses this development by the conventional figurative tree. If the specimens represented by any given portion of a branch of this tree were so constructed that under favourable circumstances they would be identical with the specimens represented by a portion of another branch, *i.e.* if any two branches could, and can, long after the common origin, merge together, then branch off again, merge together again, and so on, it would be preposterous to assume that this should never have happened. But if we thus should have to concede the possibility that the lines of ancestors of any two forms of plants or animals, say of the lion and the giraffe, were such that they first became widely divergent, then identical, then again widely divergent, not only the figurative tree, but also the kind of evolution it is meant to illustrate, would be pure nonsense. Therefore we take it that we are actually agreed upon that part of our definition which says that from a certain point a branch of the tree *cannot* merge together again with any other branch; now, if we call every form which has reached this degree of development *specifically* distinct, we have an absolute distinction between species and the lower degrees of development.

The question of specific distinctness or non-distinctness is therefore twofold: first one of morphological, and second one of physiological difference. As the systematist is practically not able to test by experiment the presence of the second distinction, it is obvious that he never can *prove* with *certainty* from the specimens alone whether the distinguishing morphological characters they exhibit are of specific value or not. However, we are able to arrive at a probably correct conclusion without testing in each case the specific distinctness, if we take into account the way in which divarication of species comes about, and if we further compare the characters of such forms as have been tested to be specifically distinct.

For our present purposes it is quite irrelevant whether the causes of the transmutation and divarication of species are those factors which are maintained by the Neo-Darwinians to be the sole agents, or those which the Neo-Lamarckians consider to be alone effective. Hence we shall abstain from any discussion of the much contested final causes of divergent development, and shall simply ask, which is the way that leads from variability of a species to divarication of this species into more species? Our purpose allows us to simplify the question still more and to restrict the discussion to the two points: first, can a species develop into two (or more) species without isolation? secondly, can isolation as such transmute one species into two (or more)?

The most extreme kind of variability of a species logically possible is that in which the varieties composing the species are not only morphologically but also physiologically different. As upon the occurrence of such variation Romanes's theory of Physiological Selection, which we have had to allude to several times, is founded, we may be allowed to annex our notes to a short discussion of this theory as far as it bears upon our particular question.

In order to explain the infertility or restricted fertility between different species Romanes assumes that the divarication of one species into more species has something to do with the occurrence of such a variation that some individuals of a given species are not fertile with the rest of the species, but are fully fertile *inter se.* That variety, though living in the same district as the normal form of the species, will develop divergently, according to the theory, and give rise to a new species, as it is physiologically so separated from the normal individuals that intercrossing is excluded. Is this conclusion correct?

We have seen above that aberrational individuals occur again and again among the normal specimens; if therefore a physiological variety such as Romanes's theory demands occurs once, a species is able to produce it again and again, as long as the circumstances under which the species lives do not change. But to make the case as favourable as possible we will assume that the normal individuals, which may be designated as N, gave birth to the variety V only once, so that if all the specimens of the variety were killed the variety would never reappear. Now, the offspring of the variety V will in the first and following broods belong either all to the variety V, or partly to the variety V and partly to the normal form N. The first assumption nobody can admit to occur, as this would mean that V is a species suddenly branched off from N, and as further we should have, instead of the explanation of the phenomenon of sterility between species which it is the aim of the theory to give, merely the statement that species V has sprung up among the individuals of species N with which it is infertile. Hence we have to do only with the second case, that part of the offspring of V, at least part of the first brood after the origin of V, belong to N; these offspring of V we will designate Nv in order to indicate that, though they are normal, they are the immediate descendants of parents with varietal characters. Nv cross *inter se* and with N, not with V; which characters will the offspring of Nv have, which itself, we repeat it, is the descendant of V? The offspring of Nv could be either all identical with Nv $(=N)$, or partly identical with Nv and partly with V. The first alternative means that each specimen of V produces two groups of individuals, Vv and Nv, of which one group (Nv) never will give rise to a form similar to its parent-form V, while the other group (Vv) produces both the parent- and grand-parent-form. Although the assumption here made, that some of the offspring of one specimen breed perfectly true (Nv), while the other offspring do not breed true, is quite at variance with our experience, and therefore not acceptable to any naturalist, we will nevertheless accept the assumption for the sake of argument. As V breeds in and in, according to that assumption, it is argued that in the course of time V will become so modified that it will also breed true like N and then be specifically distinct. Apart from Nv and V here being already two species from the beginning, one (Nv) breeding true, the other (V) producing *per saltum* in every generation some specimens of Nv, an illustration will show at once that before the above-mentioned modification is effected the variety V will altogether be swamped away. Let us assume (1) that in an isolated district two hundred specimens of a certain species (one hundred of each sex) could find subsistence; (2) that each *female* would produce ten *females* and ten *males*; (3) that at a given time one-tenth of the specimens conformed to the variety V, *i.e.* were sterile with the other nine-tenths (N), but fertile *inter se*; and (4) that 80 per cent. of the offspring of V belonged to V, the other 20 per cent. to N, which breeds true,—for convenience we shall take into account only the *females*,—the numbers of the forms N and V in the successive broods would be as follows:—

	i.	ii.	iii.	iv.	....
N ♀	90	92	94	95	....
V ♀	10	8	6	5	....

We see that the number of specimens of V diminishes, and that extinction of is physiologically so separated from the normal individuals that intercrossing is excluded. Is this conclusion correct?

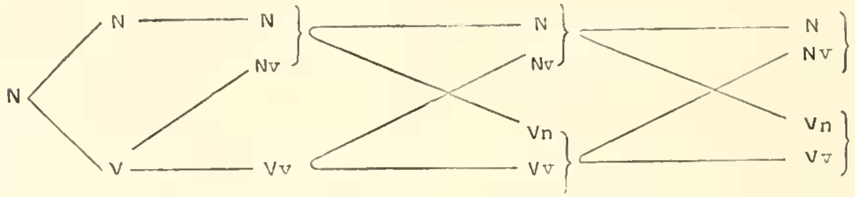
We have seen above that aberrational individuals occur again and again among the normal specimens; if therefore a physiological variety such as Romanes's theory demands occurs once, a species is able to produce it again and again, as long as the circumstances under which the species lives do not change. But to make the case as favourable as possible we will assume that the normal individuals, which may be designated as N, gave birth to the variety V only once, so that if all the specimens of the variety were killed the variety would never reappear. Now, the offspring of the variety V will in the first and following broods belong either all to the variety V, or partly to the variety V and partly to the normal form N. The first assumption nobody can admit to occur, as this would mean that V is a species suddenly branched off from N, and as further we should have, instead of the explanation of the phenomenon of sterility between species which it is the aim of the theory to give, merely the statement that species V has sprung up among the individuals of species N with which it is infertile. Hence we have to do only with the second case, that part of the offspring of V, at least part of the first brood after the origin of V, belong to N; these offspring of V we will designate Nv in order to indicate that, though they are normal, they are the immediate descendants of parents with varietal characters. Nv cross *inter se* and with N, not with V; which characters will the offspring of Nv have, which itself, we repeat it, is the descendant of V? The offspring of Nv could be either all identical with Nv ($=N$), or partly identical with Nv and partly with V. The first alternative means that each specimen of V produces two groups of individuals, Vv and Nv, of which one group (Nv) never will give rise to a form similar to its parent-form V, while the other group (Vv) produces both the parent- and grand-parent-form. Although the assumption here made, that some of the offspring of one specimen breed perfectly true (Nv), while the other offspring do not breed true, is quite at variance with our experience, and therefore not acceptable to any naturalist, we will nevertheless accept the assumption for the sake of argument. As V breeds in and in, according to that assumption, it is argued that in the course of time V will become so modified that it will also breed true like N and then be specifically distinct. Apart from Nv and V here being already two species from the beginning, one (Nv) breeding true, the other (V) producing *per saltum* in every generation some specimens of Nv, an illustration will show at once that before the above-mentioned modification is effected the variety V will altogether be swamped away. Let us assume (1) that in an isolated district two hundred specimens of a certain species (one hundred of each sex) could find subsistence; (2) that each *female* would produce ten *females* and ten *males*; (3) that at a given time one-tenth of the specimens conformed to the variety V, *i.e.* were sterile with the other nine-tenths (N), but fertile *inter se*; and (4) that 80 per cent. of the offspring of V belonged to V, the other 20 per cent. to N, which breeds true,—for convenience we shall take into account only the *females*,—the numbers of the forms N and V in the successive broods would be as follows:—

	i.	ii.	iii.	iv.	....
N♀	90	92	94	95	....
V♀	10	8	6	5	....

We see that the number of specimens of V diminishes, and that extinction of

V must soon be the result, if at the first appearance of *V* the number of individuals of this variety was not very great. With every successive brood the percentage of varietal specimens produced by *V* will become higher, and to make up for this we have assumed that the very first specimens of *V* produced already 80 per cent. of the varietal form.

There remains now only the second alternative, that *Nv* as the descendant of *V* produces both *V* and *N*, which agrees with what we know of the propagation of varieties which occur among normal specimens, and hence is the only acceptable alternative. The offspring *Vn* of *Nv* crossing with *V* will bring the blood of *Nv* and *N*, which interbreed, into *V*, just as *Nv* (as the offspring of *V*) brings the blood of *V* into *N*, and this would go on as long as *V* and *N* exist together in the same locality. Though *N* and *V* are mutually sterile, the blood of *N* comes into *V* by means of *Vn*, and the blood of *V* into *N* by means of *Nv*; this *indirect intercrossing* will completely annihilate the effect of the assumed mutual sterility of *N* and *V*. The following diagram will serve to illustrate these lines :—



It can easily be shown that after a certain time *N* and *V* will occur in equal numbers.*

The physiological selection will, therefore, in no case result in divarication of a species into two, but the outcome of the physiological variation will be either dimorphism of the species, when both the normal and the varietal form are equally favoured in respect to the circumstances of life, or extinction of that form which is the least favoured. If however the most favourable kind of variation does not lead to the origin of a new species beside the parent one, no other variation will lead to this end. Hence we must conclude that a divarication of a species into two or more species cannot come about so long as the divergent varieties live so together that a direct or indirect intercrossing is not prevented.

Having thus disposed of the possibility of the divarication of species without the help of some kind of local separation, we have to consider the other question : whether local separation as such can be able to give origin to a variety and to transform a variety into a species. The theory of isolation as promoted by Wagner says that the peculiar characters of some isolated specimens will by breeding in and in finally be transmitted to all the descendants of those specimens, and their degree of divergency become in the course of time so much higher that these descendants represent a new species.

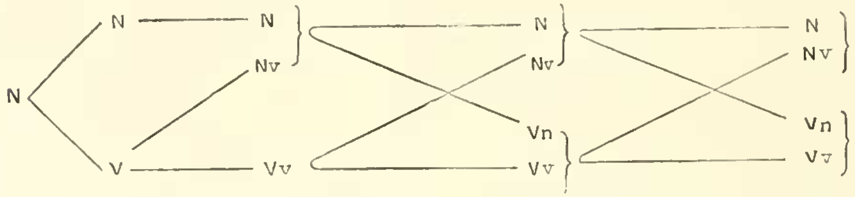
Experiments teach us that aberrant specimens of a species occurring amongst the normal specimens produce, when crossed together, offspring which partly are of the normal, partly of the varietal form of the species ; from black specimens of the moths *Amphidasis betularius* and *Liparis monacha* are obtained both black and white individuals. To make the circumstances most favourable for the eventual

---

* Murphy, *Habit and Intelligence*, London, 1879. p. 241.

V must soon be the result, if at the first appearance of *V* the number of individuals of this variety was not very great. With every successive brood the percentage of varietal specimens produced by *V* will become higher, and to make up for this we have assumed that the very first specimens of *V* produced already 80 per cent. of the varietal form.

There remains now only the second alternative, that *Nv* as the descendant of *V* produces both *V* and *N*, which agrees with what we know of the propagation of varieties which occur among normal specimens, and hence is the only acceptable alternative. The offspring *Vn* of *Nv* crossing with *V* will bring the blood of *Nv* and *N*, which interbreed, into *V*, just as *Nv* (as the offspring of *V*) brings the blood of *V* into *N*, and this would go on as long as *V* and *N* exist together in the same locality. Though *N* and *V* are mutually sterile, the blood of *N* comes into *V* by means of *Vn*, and the blood of *V* into *N* by means of *Nv*; this *indirect intercrossing* will completely annihilate the effect of the assumed mutual sterility of *N* and *V*. The following diagram will serve to illustrate these lines:—



It can easily be shown that after a certain time *N* and *V* will occur in equal numbers.*

The physiological selection will, therefore, in no case result in divarication of a species into two, but the outcome of the physiological variation will be either dimorphism of the species, when both the normal and the varietal form are equally favoured in respect to the circumstances of life, or extinction of that form which is the least favoured. If however the most favourable kind of variation does not lead to the origin of a new species beside the parent one, no other variation will lead to this end. Hence we must conclude that a divarication of a species into two or more species cannot come about so long as the divergent varieties live so together that a direct or indirect intercrossing is not prevented.

Having thus disposed of the possibility of the divarication of species without the help of some kind of local separation, we have to consider the other question: whether local separation as such can be able to give origin to a variety and to transform a variety into a species. The theory of isolation as promoted by Wagner says that the peculiar characters of some isolated specimens will by breeding in and in finally be transmitted to all the descendants of those specimens, and their degree of divergency become in the course of time so much higher that these descendants represent a new species.

Experiments teach us that aberrant specimens of a species occurring amongst the normal specimens produce, when crossed together, offspring which partly are of the normal, partly of the varietal form of the species; from black specimens of the moths *Amphidasis betularius* and *Liparis monacha* are obtained both black and white individuals. To make the circumstances most favourable for the eventual divergent development of the variety we will assume (1) that a number of varietal specimens are *completely* isolated from the rest of the species ; (2) that 80 per cent. of the offspring of these specimens belong to the varietal form. The specimens now have to propagate under the further premiss (3) that the normal and the varietal forms exist under exactly the same conditions of life, so that every other transmuting factor besides mechanical isolation is excluded. By mechanical isolation we understand a separation of the animals or plants in question by a mechanical barrier, so that an intercrossing with the original stock is prevented; experimentally the case could be demonstrated by rearing wingless animals side by side, but separated by an adequate fence. Under the above premisses ten *females* of a variety, each producing twenty *females*, kept in an enclosure representing the isolated locality, would give birth to a hundred and sixty *females* of the varietal (*V*) and forty of the normal form (*N*). If the latter produce also each twenty *females*, of which 80 per cent. might be taken as normal and 20 per cent. as varietal, and if the locality is fit to provide food for a thousand *females* (and a thousand *males*, which are not taken into account), the numbers of both forms would in the succeeding broods be as follows :—

---

* Murphy, *Habit and Intelligence*, London, 1879. p. 241.

	i.	ii.	iii.	iv.	v.
N	—	40	320	392	435
V	10	160	680	608	565

The result is here again that after a small number of broods both the varietal and normal forms will exist in equal numbers in the isolated district. The varietal form can never become the sole inhabitant of that district unless the circumstances of life are such that the normal form is less favoured by them, *i.e.* unless there is some transmuting factor active besides isolation. Isolation as such is not an active factor which produces a character, but is a factor which merely preserves a character produced by some other factor; isolation has, therefore, no direct effect. The reason that the effect of isolation has by many authors been so much overestimated is so obvious that we scarcely need mention it : the differences exhibited by geographically isolated forms of the same species are often attributed to the direct effect of isolation, because isolation and morphological difference were seen to be always associated, while no other transmuting factor seemed to be obvious to those who were unacquainted with the experiments made in this direction. Apart from experiments, there are many geographical races which, on closer examination, show at once that their characters cannot be the outcome of the isolation of some ancestral specimens which accidentally exhibited the respective distinguishing character. Wallace* was the first to draw attention to a peculiarity common to a great many species of butterflies on the island of Celebes : these species or varieties have much longer and more falcate forewings than the races from the other islands of the Indo-Australian region. On the island of Sumba, which lies south of Flores, that character is also found in some species. The Chinese races of butterflies and moths have generally the black colour more extended than the respective Indian races. The butterflies and moths of Sumatra and Borneo † are mostly much darker than the races of the same species from Malacca and Java. The Queenslandian races are often pale, those from the Kei Islands have the markings often restricted, and so on.

---

* *Proc. Linn. Soc. Lond.* XXV. p. 18.

† Hagen, *Iris* 1894. p. 17.

divergent development of the variety we will assume (1) that a number of varietal specimens are *completely* isolated from the rest of the species; (2) that 80 per cent. of the offspring of these specimens belong to the varietal form. The specimens now have to propagate under the further premiss (3) that the normal and the varietal forms exist under exactly the same conditions of life, so that every other transmuting factor besides mechanical isolation is excluded. By mechanical isolation we understand a separation of the animals or plants in question by a mechanical barrier, so that an intercrossing with the original stock is prevented; experimentally the case could be demonstrated by rearing wingless animals side by side, but separated by an adequate fence. Under the above premisses ten *females* of a variety, each producing twenty *females*, kept in an enclosure representing the isolated locality, would give birth to a hundred and sixty *females* of the varietal (*V*) and forty of the normal form (*N*). If the latter produce also each twenty *females*, of which 80 per cent. might be taken as normal and 20 per cent. as varietal, and if the locality is fit to provide food for a thousand *females* (and a thousand *males*, which are not taken into account), the numbers of both forms would in the succeeding broods be as follows :—

	i.	ii.	iii.	iv.	v.
N	—	40	320	392	435
V	10	160	680	608	565

The result is here again that after a small number of broods both the varietal and normal forms will exist in equal numbers in the isolated district. The varietal form can never become the sole inhabitant of that district unless the circumstances of life are such that the normal form is less favoured by them, *i.e.* unless there is some transmuting factor active besides isolation. Isolation as such is not an active factor which produces a character, but is a factor which merely preserves a character produced by some other factor; isolation has, therefore, no direct effect. The reason that the effect of isolation has by many authors been so much overestimated is so obvious that we scarcely need mention it: the differences exhibited by geographically isolated forms of the same species are often attributed to the direct effect of isolation, because isolation and morphological difference were seen to be always associated, while no other transmuting factor seemed to be obvious to those who were unacquainted with the experiments made in this direction. Apart from experiments, there are many geographical races which, on closer examination, show at once that their characters cannot be the outcome of the isolation of some ancestral specimens which accidentally exhibited the respective distinguishing character. Wallace* was the first to draw attention to a peculiarity common to a great many species of butterflies on the island of Celebes: these species or varieties have much longer and more falcate forewings than the races from the other islands of the Indo-Australian region. On the island of Sumba, which lies south of Flores, that character is also found in some species. The Chinese races of butterflies and moths have generally the black colour more extended than the respective Indian races. The butterflies and moths of Sumatra and Borneo † are mostly much darker than the races of the same species from Malacca and Java. The Queenslandian races are often pale, those from the Kei Islands have the markings often restricted, and so on.

---

* *Proc. Linn. Soc. Lond.* XXV. p. 18.

† Hagen, *Iris* 1894. p. 17.

Characters like these, common to a multitude of racial forms living in one isolated district, cannot be accounted for by a direct effect of isolation : it would be almost ridiculous to assume that the first specimens of a great number of species which came to Celebes had all long and falcate wings, while the specimens dispersed over the neighbouring groups of islands had short wings : or that the first specimens which came to Sumatra and Borneo were dark, while the individuals of the same species which migrated to Java were in so many cases less black.

We now have seen that the geographical isolation of aberrant specimens has not been and is not the means of the divarication of species, and that the effect of the transmuting factors acting upon the specimens of a species within the same locality is at the highest marked polymorphism ; therefore there is only one way possible by which the divarication of a species into two or more can come about—that is, the combination of isolation and transmuting factors. *The isolation of one or more* (Neo-Darwinian and Neo-Lamarckian) *factors* is the means by which the specimens of a species which are subjected to these isolated factors, whichever they may be, become different from those specimens which stand under other influences, no matter whether the first specimens which became isolated as to the transmuting factors were normal or aberrational. This assumption corresponds completely with the result of experiments, and explains all the peculiarities in the characters of geographical races and representative species. And we shall see in the third part of this paper that there are instances in which the geographical isolation can be very incomplete, and in which, nevertheless, the divergent development will lead to specific distinctness of the biologically isolated specimens.

The geographical races thus produced we must assume to be first inconstant, to become more and more constant and divergent by the incessant influence of the transmuting factors, and to develop finally into a form which is so modified that it never will fuse either with the parent-form or the sister-forms, and that it therefore agrees with the definition of the term "species."

As this kind of divarication of species is the only possible* one, and hence geographical polymorphism of a species the beginning of the ramification into more species, the study of localised varieties is of the greatest importance in respect to the theory of evolution ; the study of geographical races, or subspecies, or incipient species, is a study of the origin of species. The meaning of the term "subspecies,"† nowadays generally applied to geographical or localised forms, is evolutionistic, and, in fact, the only evolutionistic idea which has penetrated into that work of systematists which is purely diagnostic. Every scientist who pretends to be an evolutionist must perceive the importance of subspecies. Whoever persistently ignores the existence of subspecific characters ought to have the courage which I admire in Charles Oberthür—great courage it certainly requires to defend a standpoint against the bulk of naturalists—to define the species as a created entity.

Eimer, *Artbildung und Verwandtschaft bei Schmetterlingen*, gives beautiful examples of the various degrees of divergency of localised varieties. Whether only one or a few specimens exhibit in a given locality a character not found elsewhere ; whether a greater number of individuals in a certain district are characterised by a

---

* It is scarcely necessary to add that the area to which a certain transmuting factor is restricted need not be a political or physiographical district.

† This term had already been applied to geographical races before the appearance of Darwin's *Origin of Species*.

Characters like these, common to a multitude of racial forms living in one isolated district, cannot be accounted for by a direct effect of isolation : it would be almost ridiculous to assume that the first specimens of a great number of species which came to Celebes had all long and falcate wings, while the specimens dispersed over the neighbouring groups of islands had short wings : or that the first specimens which came to Sumatra and Borneo were dark, while the individuals of the same species which migrated to Java were in so many cases less black.

We now have seen that the geographical isolation of aberrant specimens has not been and is not the means of the divarication of species, and that the effect of the transmuting factors acting upon the specimens of a species within the same locality is at the highest marked polymorphism ; therefore there is only one way possible by which the divarication of a species into two or more can come about—that is, the combination of isolation and transmuting factors. *The isolation of one or more* (Neo-Darwinian and Neo-Lamarckian) *factors* is the means by which the specimens of a species which are subjected to these isolated factors, whichever they may be, become different from those specimens which stand under other influences, no matter whether the first specimens which became isolated as to the transmuting factors were normal or aberrational. This assumption corresponds completely with the result of experiments, and explains all the peculiarities in the characters of geographical races and representative species. And we shall see in the third part of this paper that there are instances in which the geographical isolation can be very incomplete, and in which, nevertheless, the divergent development will lead to specific distinctness of the biologically isolated specimens.

The geographical races thus produced we must assume to be first inconstant, to become more and more constant and divergent by the incessant influence of the transmuting factors, and to develop finally into a form which is so modified that it never will fuse either with the parent-form or the sister-forms, and that it therefore agrees with the definition of the term "species."

As this kind of divarication of species is the only possible* one, and hence geographical polymorphism of a species the beginning of the ramification into more species, the study of localised varieties is of the greatest importance in respect to the theory of evolution ; the study of geographical races, or subspecies, or incipient species, is a study of the origin of species. The meaning of the term "subspecies,"† nowadays generally applied to geographical or localised forms, is evolutionistic, and, in fact, the only evolutionistic idea which has penetrated into that work of systematists which is purely diagnostic. Every scientist who pretends to be an evolutionist must perceive the importance of subspecies. Whoever persistently ignores the existence of subspecific characters ought to have the courage which I admire in Charles Oberthür—great courage it certainly requires to defend a standpoint against the bulk of naturalists—to define the species as a created entity.

Eimer, *Artbildung und Verwandtschaft bei Schmetterlingen*, gives beautiful examples of the various degrees of divergency of localised varieties. Whether only one or a few specimens exhibit in a given locality a character not found elsewhere ; whether a greater number of individuals in a certain district are characterised by a peculiarity not met with, or rarely met with, in other districts; whether all the localised specimens are different from the rest of the species; whether a localised variety is or is not connected with the other varieties by intergraduate specimens,—in every case the presence of a localised peculiarity indicates that the individuals inhabiting the respective locality are on the way to develop divergently in consequence of some biological peculiarity of the locality. All these degrees of divergency are distinguished from that higher degree which we have taken as the criterion of specific distinctness by not conforming to the physiological part of our definition of species. By experiments it has been proved * that geographical forms lose their distinguishing characters and fuse together with other forms of the same species. Therefore, if all the coexistent specimens of a species were at our disposal, the definition of the term "subspecies" would be as follows:—

---

* It is scarcely necessary to add that the area to which a certain transmuting factor is restricted need not be a political or physiographical district.

† This term had already been applied to geographical races before the appearance of Darwin's *Origin of Species*.

A subspecies is a localised group of individuals of a species the mean of the characters of which is different from the mean of the characters of all the other localised groups, and which will, under favourable circumstances, fuse together with other groups.

However, the material contained in collections is, compared with the actual number of specimens existing of each variety, extremely meagre, though nowadays systematists comprehend more and more that a few specimens of each species are insufficient for a serious study, and hence try to bring together long series from every locality. The conclusions, in respect to variation, which we draw from the inadequate material we have to work with, must necessarily often be erroneous. If, for example, our series shows a variation of a character (expressed in numbers) between twenty and fifty, there may, in fact, exist individuals which stand outside these limits. Rare varietal specimens, which hitherto have been found only in a certain locality, may very well occur elsewhere; a certain variety may appear to us more common in one locality than in another, and hence the mean of the characters in the first locality to be different from the mean in other localities, because a collector paid more attention to varietal specimens in the first locality. This imperfectness of our knowledge we have to take into account, and we must, therefore, restrict the application of the term "subspecies" in order to avoid deception as far as possible.

The above definition has not had regard to the degree of divergency attained by the localised form. Now, we ask, which then is the lower limit of application of the term "subspecies"? The diversity which the sexes exhibit in respect to localised variation gives us the answer. We know a good many cases in which the *males* are in various districts not distinguishable, while the *females* are very different, and cases in which the variation takes place in the *male* sex and not in the *female* sex. For illustration we refer to the following insects: *Papilio semperi*, from the Philippine Islands, varies in the *female* sex according to locality, while the *males* from the various islands, in spite of individual variability, are not distinguishable; *Papilio oenomaus*, from Timor and Wetter, is on these two islands the same in the *male* sex, while the *females* are conspicuously different: and so it is with *Papilio phestus*, from New Britain, New Ireland, and the Solomon Islands. If we apply in these cases, the importance of which we shall soon endeavour to show, the term "subspecies," we have a rule which can guide us in all other cases—namely, as the numbers of specimens of each sex can be taken as being (roughly) equal, we shall have to use the term "subspecies" when a localised variation is such that about half

* Kerner *Gute und Schlechte Arten*; Weismann *Studien zur Descendenztheorie.*

peculiarity not met with, or rarely met with, in other districts; whether all the localised specimens are different from the rest of the species; whether a localised variety is or is not connected with the other varieties by intergraduate specimens,—in every case the presence of a localised peculiarity indicates that the individuals inhabiting the respective locality are on the way to develop divergently in consequence of some biological peculiarity of the locality. All these degrees of divergency are distinguished from that higher degree which we have taken as the criterion of specific distinctness by not conforming to the physiological part of our definition of species. By experiments it has been proved * that geographical forms lose their distinguishing characters and fuse together with other forms of the same species. Therefore, if all the coexistent specimens of a species were at our disposal, the definition of the term "subspecies" would be as follows:—

A subspecies is a localised group of individuals of a species the mean of the characters of which is different from the mean of the characters of all the other localised groups, and which will, under favourable circumstances, fuse together with other groups.

However, the material contained in collections is, compared with the actual number of specimens existing of each variety, extremely meagre, though nowadays systematists comprehend more and more that a few specimens of each species are insufficient for a serious study, and hence try to bring together long series from every locality. The conclusions, in respect to variation, which we draw from the inadequate material we have to work with, must necessarily often be erroneous. If, for example, our series shows a variation of a character (expressed in numbers) between twenty and fifty, there may, in fact, exist individuals which stand outside these limits. Rare varietal specimens, which hitherto have been found only in a certain locality, may very well occur elsewhere; a certain variety may appear to us more common in one locality than in another, and hence the mean of the characters in the first locality to be different from the mean in other localities, because a collector paid more attention to varietal specimens in the first locality. This imperfectness of our knowledge we have to take into account, and we must, therefore, restrict the application of the term "subspecies" in order to avoid deception as far as possible.

The above definition has not had regard to the degree of divergency attained by the localised form. Now, we ask, which then is the lower limit of application of the term "subspecies"? The diversity which the sexes exhibit in respect to localised variation gives us the answer. We know a good many cases in which the *males* are in various districts not distinguishable, while the *females* are very different, and cases in which the variation takes place in the *male* sex and not in the *female* sex. For illustration we refer to the following insects: *Papilio semperi*, from the Philippine Islands, varies in the *female* sex according to locality, while the *males* from the various islands, in spite of individual variability, are not distinguishable; *Papilio oenomaus*, from Timor and Wetter, is on these two islands the same in the *male* sex, while the *females* are conspicuously different: and so it is with *Papilio phestus*, from New Britain, New Ireland, and the Solomon Islands. If we apply in these cases, the importance of which we shall soon endeavour to show, the term "subspecies," we have a rule which can guide us in all other cases—namely, as the numbers of specimens of each sex can be taken as being (roughly) equal, we shall have to use the term "subspecies" when a localised variation is such that about half of the individuals belong to the varietal form. All lower degrees of localised variation may be termed "localised aberration" (ab. loc. = *aberratio alicuius loci*).*

---

* Kerner *Gute und Schlechte Arten*; Weismann *Studien zur Descendenztheorie.*

We have already referred to some observations which show that localised divergent development is going on under our eyes. There are certainly species which are at present stationary, and perhaps have been so for a long time; but so much is certain that nearly all the species which have a wider distribution (except a number of "globe-trotters") exhibit some kind of local variation, and that, therefore, since local variation is the beginning of the divarication of a species into more species, the more widely distributed species are at the present period actually in a state of divergent development. We have examined a great many *Lepidoptera*, both butterflies and moths, in regard to this question, and find that there are very few species which are not split up into geographical races, although the differences between the subspecies are often extremely minute. The degree of divergency depends especially on the sensibility of the species in respect to the transmuting factors, and on the degree of isolation and intensity of the latter, as well as on the degree of geographical isolation. Wingless animals, and plants without means of dispersal, are generally more easily affected and on smaller areas than animals and plants with good means of dispersal. Wingless beetles, for example, such as *Carabus*, vary enormously according to locality; in the Alps, for instance, there are a great many subspecies of *Carabus* each confined often to one mountain.

The number of subspecies into which the Indo-Australian *Papilios* have developed is very great,† and, when studying these insects, we were surprised to find that, in opposition to the general view, not the *males* but the *females* appear to be the first affected by localised transmuting factors. In *all* cases, without exception, where the distinguishing characters of a subspecies are found only in one sex, it is the *female* and not the *male* which exhibits them; and further, in those subspecies which are obviously different in all specimens of one sex, slightly or even only occasionally different in the other sex, it is again the *female* that is the more aberrant sex. If we further take into account the *local aberrations* as far as they constantly and commonly appear among the normal specimens, we have thirty-six cases among the Indo-Australian Papilios in which the localised variation is entirely or almost entirely restricted to the *female* sex, while there is not a single subspecies which is in the *male* much more different from the allies than in the *female*. In seasonal forms of Papilios the *females* again exhibit a greater amount of divergency than the *males*, a phenomenon which is strikingly illustrated by the Japanese *Papilio machaon hippocrates*. The variability is in the *females* of the Indo-Australian Papilios altogether greater than in the *males*, or, to express it biologically, the *females* are more easily affected by the causes of variation than the other sex. If localised variation is the beginning of the divarication of a species into more species, and we have seen that this is the only possible way by which divarication can come about, those phenomena, which relate especially to pattern, admit no other explanation than that, at least in all cases where the localised variation is restricted, or nearly so, to the *females*, the transmutation of the species begins in the *female* sex, and that, therefore, the *female* is in advance of the *male* in respect of the development into new species. Eimer and Fickert in their studies on the Papilios come to the opposite result; and that is, we think, due to their assumption that the original pattern of the wings of Papilios consisted of "longitudinal" bands of the individuals belong to the varietal form. All lower degrees of localised variation may be termed "localised aberration" (ab. loc. = *aberratio alicuius loci*).*

---

* See this journal, 1895. p. 180.

† See Rothschild, Nov. Zool. 1895. p. 463.

We have already referred to some observations which show that localised divergent development is going on under our eyes. There are certainly species which are at present stationary, and perhaps have been so for a long time; but so much is certain that nearly all the species which have a wider distribution (except a number of "globe-trotters") exhibit some kind of local variation, and that, therefore, since local variation is the beginning of the divarication of a species into more species, the more widely distributed species are at the present period actually in a state of divergent development. We have examined a great many *Lepidoptera*, both butterflies and moths, in regard to this question, and find that there are very few species which are not split up into geographical races, although the differences between the subspecies are often extremely minute. The degree of divergency depends especially on the sensibility of the species in respect to the transmuting factors, and on the degree of isolation and intensity of the latter, as well as on the degree of geographical isolation. Wingless animals, and plants without means of dispersal, are generally more easily affected and on smaller areas than animals and plants with good means of dispersal. Wingless beetles, for example, such as *Carabus*, vary enormously according to locality; in the Alps, for instance, there are a great many subspecies of *Carabus* each confined often to one mountain.

The number of subspecies into which the Indo-Australian *Papilios* have developed is very great,† and, when studying these insects, we were surprised to find that, in opposition to the general view, not the *males* but the *females* appear to be the first affected by localised transmuting factors. In *all* cases, without exception, where the distinguishing characters of a subspecies are found only in one sex, it is the *female* and not the *male* which exhibits them; and further, in those subspecies which are obviously different in all specimens of one sex, slightly or even only occasionally different in the other sex, it is again the *female* that is the more aberrant sex. If we further take into account the *local aberrations* as far as they constantly and commonly appear among the normal specimens, we have thirty-six cases among the Indo-Australian Papilios in which the localised variation is entirely or almost entirely restricted to the *female* sex, while there is not a single subspecies which is in the *male* much more different from the allies than in the *female*. In seasonal forms of Papilios the *females* again exhibit a greater amount of divergency than the *males*, a phenomenon which is strikingly illustrated by the Japanese *Papilio machaon hippocrates*. The variability is in the *females* of the Indo-Australian Papilios altogether greater than in the *males*, or, to express it biologically, the *females* are more easily affected by the causes of variation than the other sex. If localised variation is the beginning of the divarication of a species into more species, and we have seen that this is the only possible way by which divarication can come about, those phenomena, which relate especially to pattern, admit no other explanation than that, at least in all cases where the localised variation is restricted, or nearly so, to the *females*, the transmutation of the species begins in the *female* sex, and that, therefore, the *female* is in advance of the *male* in respect of the development into new species. Eimer and Fickert in their studies on the Papilios come to the opposite result; and that is, we think, due to their assumption that the original pattern of the wings of Papilios consisted of "longitudinal" bands standing at right angles to the veins; if Eimer had assumed that the original pattern of the wings consisted of "longitudinal" bands running in the direction of the veins,[*] he would have arrived at a "preponderance" of the *female* sex.

---

* See this journal, 1895. p. 180.

† See Rothschild, Nov. Zool. 1895. p. 463.

The degree of divergency is, in many subspecies, so minute that the peculiarity would escape even a skilled eye but for a carefully working systematist having drawn attention to it, and having fixed, so to say, the minute peculiar character by naming the subspecies. Romanes has severally referred to minute specific characters in order to confute Wallace's opinion that all specific characters are useful; as specific characters are only higher degrees of development of subspecific characters, the question whether subspecific characters have originated and are accumulated by Natural Selection is no less important than the same question in respect to specific characters. Dixon [†] and Allen [‡] give ample illustrations of the question as regards birds. Of *Lepidoptera* we mention, out of hundreds of cases, only two: *Papilio nomius* has a western subspecies (Ceylon to Assam) and an eastern subspecies (Burma, Tenasserim, Tonkin, Hainan) which are *constantly* differentiated by one minute character, namely a brown line situate in the eastern form on the praecostal vein on the underside of the hindwing, which short and thin line is absent from the specimens of the western subspecies; that this distinguishing character is indeed minute will be admitted if we add that, though it is the only constant difference of the two subspecies we can find, it has never been mentioned by any specialist until 1895, in Mr. Walter Rothschild's Revision of the Eastern Papilios.[§] *Papilio agamemnon argynnus* from the Kei Islands and *P. agamemnon neopommeranius* from Neu-Pommern differ from all the other subspecies of *agamemnon* in the hindwings being above nearly devoid of markings, which renders the two subspecies extremely similar; but there is one constant character, which can easily be perceived with the help of a lens, that distinguishes *neopommeranius* and *argynnus*: in *neopommeranius* the spots of the median row of the forewing beneath are scaled all over, while in *argynnus* the outer portion of each spot is scaleless. Though nobody can very well entertain the opinion that such differences are due to the direct action of Natural Selection, one can evade the weight of the minute distinguishing characters by the assumption that these minute characters are correlated to some other, unknown, character which is of a useful kind. *Lepidoptera*, however, furnish us with the means to repudiate this evasive answer. All those species which are said to be mimetic, and which have been quoted again and again as excellent illustrations of the marvellous effect of Natural Selection, have certain characters of colour or form which are attributed to the direct (not indirect) influence of Natural Selection. Now, if such a character varies geographically in the mimetic species and at the same locality in the imitated species by minute degrees, the minute difference between the geographical forms of the mimetic species ought logically also to be attributed to the direct action of Natural Selection. Such cases are, however, not rare among insects. We refer, for the sake of illustration, to one of the most striking examples of mimetic adaptation. *Papilio caunus* of the Malayan region has a style of marking quite unusual for a *Papilio*, and resembles another, nauseous, butterfly, *Euploea rhadamanthus*, to a surprising standing at right angles to the veins; if Eimer had assumed that the original pattern of the wings consisted of "longitudinal" bands running in the direction of the veins,[*] he would have arrived at a "preponderance" of the *female* sex.

---

[*] According to Eimer, the costae and rows of punctures on the elytra of beetles are transverse, while the bands (of *Cerambycidae*, *Cantharidae*, etc.) which stand at right angles to those rows, and which are often continuations of the transverse bands of the sterna and abdomen, must be called longitudinal.

[†] *Evolution without Natural Selection*, London, 1885.

[‡] *On the Mammals and Winter Birds of East Florida*, in *Bull. Mus. Comp. Zool.* II. 1871.

[§] Nov. Zool. 1895. p. 422.

The degree of divergency is, in many subspecies, so minute that the peculiarity would escape even a skilled eye but for a carefully working systematist having drawn attention to it, and having fixed, so to say, the minute peculiar character by naming the subspecies. Romanes has severally referred to minute specific characters in order to confute Wallace's opinion that all specific characters are useful; as specific characters are only higher degrees of development of subspecific characters, the question whether subspecific characters have originated and are accumulated by Natural Selection is no less important than the same question in respect to specific characters. Dixon [†] and Allen [‡] give ample illustrations of the question as regards birds. Of *Lepidoptera* we mention, out of hundreds of cases, only two: *Papilio nomius* has a western subspecies (Ceylon to Assam) and an eastern subspecies (Burma, Tenasserim, Tonkin, Hainan) which are *constantly* differentiated by one minute character, namely a brown line situate in the eastern form on the praecostal vein on the underside of the hindwing, which short and thin line is absent from the specimens of the western subspecies; that this distinguishing character is indeed minute will be admitted if we add that, though it is the only constant difference of the two subspecies we can find, it has never been mentioned by any specialist until 1895, in Mr. Walter Rothschild's Revision of the Eastern Papilios.[§] *Papilio agamemnon argynnus* from the Kei Islands and *P. agamemnon neopommeranius* from Neu-Pommern differ from all the other subspecies of *agamemnon* in the hindwings being above nearly devoid of markings, which renders the two subspecies extremely similar; but there is one constant character, which can easily be perceived with the help of a lens, that distinguishes *neopommeranius* and *argynnus*: in *neopommeranius* the spots of the median row of the forewing beneath are scaled all over, while in *argynnus* the outer portion of each spot is scaleless. Though nobody can very well entertain the opinion that such differences are due to the direct action of Natural Selection, one can evade the weight of the minute distinguishing characters by the assumption that these minute characters are correlated to some other, unknown, character which is of a useful kind. *Lepidoptera*, however, furnish us with the means to repudiate this evasive answer. All those species which are said to be mimetic, and which have been quoted again and again as excellent illustrations of the marvellous effect of Natural Selection, have certain characters of colour or form which are attributed to the direct (not indirect) influence of Natural Selection. Now, if such a character varies geographically in the mimetic species and at the same locality in the imitated species by minute degrees, the minute difference between the geographical forms of the mimetic species ought logically also to be attributed to the direct action of Natural Selection. Such cases are, however, not rare among insects. We refer, for the sake of illustration, to one of the most striking examples of mimetic adaptation. *Papilio caunus* of the Malayan region has a style of marking quite unusual for a *Papilio*, and resembles another, nauseous, butterfly, *Euploea rhadamanthus*, to a surprising degree. The three Malayan subspecies of *Papilio caunus*, inhabiting the first Malacca and Sumatra, the second Borneo, and the third Java, differ from one another by closer examination in the size of the white markings; the differences are, however, so slight that they do not affect the general aspect of the specimens; in fact, the Java *caunus* resembles the Bornean *rhadamanthus* just as much as the Bornean *caunus* does. The difference between the three *caunus*-forms are certainly not such that if the differences were altogether absent the specimens would be less protected; there are, to be sure, very few cases of mimicry in which the resemblance of the mimetic and imitated species is greater than that of any of the three *caunus*-forms with any of the three *rhadamanthus*-forms. If, therefore, mimicry is of value to the imitating species in all cases where the resemblance is of a much more superficial kind, we cannot see why it was necessary at all to have the white markings of the Borneo *caunus*, compared with the Malacca and Java *caunus*, a little reduced. Further, though the resemblance between the species in question is very great, there are still differences in markings between the mimetic and the imitating species in each locality which are greater than the differences between the three *caunus*-forms. It certainly requires a great deal of faith in the omnipotency of Natural Selection to believe that the slight reduction of the white markings in the Borneo form of *Papilio caunus* is due to a survival of those specimens of *caunus* in which the white markings were a little smaller than usual; the enemies of *caunus* to which we attribute the execution of the selection then must have been possessed of a much keener power of discrimination of markings than the entomologists who, until the appearance of Mr. Walter Rothschild's Revision of the Eastern Papilios, treated the Bornean *caunus* as identical with the Java *caunus* as figured by Westwood! If we, however, admit that the slight distinguishing characters of the three Malayan *caunus*-forms cannot possibly be due to the action of Natural Selection, but must be the effect of some other transmuting factor, it is evident that also in all other cases of minute distinguishing characters we need not refer to Natural Selection as the cause of the minute difference. The presence of minute distinguishing characters allows, therefore, a restriction of the possible causes of the divergency of the respective forms; and, as we thus have to admit the importance of insignificant distinctions in respect to evolution, it will be obvious that the importance increases as the degree of distinctness decreases.

---

[*] According to Eimer, the costae and rows of punctures on the elytra of beetles are transverse, while the bands (of *Cerambycidae*, *Cantharidae*, etc.) which stand at right angles to those rows, and which are often continuations of the transverse bands of the sterna and abdomen, must be called longitudinal.

[†] *Evolution without Natural Selection*, London, 1885.

[‡] *On the Mammals and Winter Birds of East Florida*, in *Bull. Mus. Comp. Zool.* II. 1871.

[§] Nov. Zool. 1895. p. 422.

We have said above that we take as the lower limit of the application of the term "subspecies" such cases in which about half of the individuals are characterised by some peculiarity: which is the upper limit? or, when have we to begin to call a form specifically distinct? According to our definitions of the terms "species" and "subspecies," the distinction between subspecies and species is a biological one, the presence of which, as mentioned on p. 442, we systematists are not able to directly prove or disprove from the material we are working with. As we know now from experiments and careful field observations that morphologically very different forms, connected or not by intergradations, can, in spite of the conspicuous differences, be one species (individual and seasonal polymorphism, heterogenesis, etc.), it is *a priori* evident that also geographically separated forms, in spite of their being morphologically distinct and in spite of their not being connected with one another by intergradations, can very well be subspecies of one species, *i.e.* can under favourable circumstances fuse into one form. The actual proof of specific distinctness the systematist as such cannot bring; we species-makers do, in fact, not pretend, at least many of us do not, that in every case the form which we pronounce to be degree. The three Malayan subspecies of *Papilio caunus*, inhabiting the first Malacca and Sumatra, the second Borneo, and the third Java, differ from one another by closer examination in the size of the white markings ; the differences are, however, so slight that they do not affect the general aspect of the specimens; in fact, the Java *caunus* resembles the Bornean *rhadamanthus* just as much as the Bornean *caunus* does. The difference between the three *caunus*-forms are certainly not such that if the differences were altogether absent the specimens would be less protected; there are, to be sure, very few cases of mimicry in which the resemblance of the mimetic and imitated species is greater than that of any of the three *caunus*-forms with any of the three *rhadamanthus*-forms. If, therefore, mimicry is of value to the imitating species in all cases where the resemblance is of a much more superficial kind, we cannot see why it was necessary at all to have the white markings of the Borneo *caunus*, compared with the Malacca and Java *caunus*, a little reduced. Further, though the resemblance between the species in question is very great, there are still differences in markings between the mimetic and the imitating species in each locality which are greater than the differences between the three *caunus*-forms. It certainly requires a great deal of faith in the omnipotency of Natural Selection to believe that the slight reduction of the white markings in the Borneo form of *Papilio caunus* is due to a survival of those specimens of *caunus* in which the white markings were a little smaller than usual; the enemies of *caunus* to which we attribute the execution of the selection then must have been possessed of a much keener power of discrimination of markings than the entomologists who, until the appearance of Mr. Walter Rothschild's Revision of the Eastern Papilios, treated the Bornean *caunus* as identical with the Java *caunus* as figured by Westwood ! If we, however, admit that the slight distinguishing characters of the three Malayan *caunus*-forms cannot possibly be due to the action of Natural Selection, but must be the effect of some other transmuting factor, it is evident that also in all other cases of minute distinguishing characters we need not refer to Natural Selection as the cause of the minute difference. The presence of minute distinguishing characters allows, therefore, a restriction of the possible causes of the divergency of the respective forms; and, as we thus have to admit the importance of insignificant distinctions in respect to evolution, it will be obvious that the importance increases as the degree of distinctness decreases.

We have said above that we take as the lower limit of the application of the term "subspecies" such cases in which about half of the individuals are characterised by some peculiarity : which is the upper limit ? or, when have we to begin to call a form specifically distinct ? According to our definitions of the terms "species" and "subspecies," the distinction between subspecies and species is a biological one, the presence of which, as mentioned on p. 442, we systematists are not able to directly prove or disprove from the material we are working with. As we know now from experiments and careful field observations that morphologically very different forms, connected or not by intergradations, can, in spite of the conspicuous differences, be one species (individual and seasonal polymorphism, heterogenesis, etc.), it is *a priori* evident that also geographically separated forms, in spite of their being morphologically distinct and in spite of their not being connected with one another by intergradations, can very well be subspecies of one species, *i.e.* can under favourable circumstances fuse into one form. The actual proof of specific distinctness the systematist as such cannot bring ; we species-makers do, in fact, not pretend, at least many of us do not, that in every case the form which we pronounce to be a species is really a species ; we work, or ought to work, with the mental reservation that the specific distinctness of our *species novae* deduced from morphological differences will be corroborated by biology (in the widest sense). The work a systematist has to do is twofold : above all, he is a registrar of facts observed upon the body of individuals, and secondly he has to draw conclusions from those facts.

All our knowledge of nature is based upon the knowledge of single phenomena. In Natural History the base of our knowledge is the individual : the characters of individuals and sums of individuals are the A B C of this science ; they are to the naturalist what words are to the philologer. To render the characters clear is the first task to be solved ; before this task is completed we are not able to draw correct conclusions. Although nowadays the recorder of facts, the diagnosticist, does not rank high in science, every theory in Natural History depends especially on the correctness of the facts furnished by the diagnosticist ; when that record lacks correctness the theory based upon it must break down. As an excellent illustration of this we may regard Weismann's theory* of "Phyletic Parallelism in Metamorphic Species," as far as it asserts the existence of an incongruity in the classification of *Lepidoptera* based on larval or based on imaginal characters. The "*Rhopalocera*" are by no means a sharply defined group in the imago state ; neither the erect position of the wing of the resting butterfly and the colour of the wings, nor the clubbed antennae, are characters applying to all "*Rhopalocera*" and exclusively to *Rhopalocera* ; and as there is no single character by which all the *Rhopalocera* are distinguished from all other *Lepidoptera*, we can also not expect that the larvae of *Rhopalocera* form a sharply defined group distinguished as a whole from all other Lepidopterous larvae. The apparent incongruity in the classification according to the larval or imaginal state of "*Bombycidae*" and "*Notodontidae*" again is not due to an incongruent development of larvae and imagines, but to the fact that Lepidopterists have placed in these (and other) families the most heterogeneous things in consequence of an entirely inadequate knowledge of the forms classified.

We learn from this illustration first that diagnostic work is the true basis of evolutionistic theories and hence of the highest importance, and secondly that the record of facts must be exact. Huxley says that the record of facts is not scientific if the facts do not permit of the drawing of general conclusions. In the above case the blame is much more on the side of the systematists who gave the clubbed antennae as distinguishing character of butterflies, than on the side of Weismann who accepted this statement as correct. If, therefore, diagnostic work is intended to meet the claim of furnishing facts from which general conclusions as to evolution (classification, variation, etc.) can safely be drawn, or if a diagnosticist claims to have his work regarded as scientific, it must be well distinguished between the description of the characters of individuals and the statement of an opinion deduced by the diagnosticist from the characters of the individuals ; the record of the characters of individuals, or the statement of facts, ought to precede the statement of the personal conclusion, which perhaps is entirely wrong. In the case of species and lower degrees of divergency diagnosticists mostly lose sight of this ; when we describe a number of individuals as belonging to a new species we present very often to the reader, not the characters of the specimens, but a ready-made conclusion which asserts (1) that the specimens are specifically identical, and (2) that the species varies in colour, markings, structure, and size to such and such an extent. The specific a species is really a species ; we work, or ought to work, with the mental reservation that the specific distinctness of our *species novae* deduced from morphological differences will be corroborated by biology (in the widest sense). The work a systematist has to do is twofold : above all, he is a registrar of facts observed upon the body of individuals, and secondly he has to draw conclusions from those facts.

---

* Weismann, *Studies in the Theory of Descent*, London, 1882, II. p. 132.

All our knowledge of nature is based upon the knowledge of single phenomena. In Natural History the base of our knowledge is the individual : the characters of individuals and sums of individuals are the A B C of this science ; they are to the naturalist what words are to the philologer. To render the characters clear is the first task to be solved ; before this task is completed we are not able to draw correct conclusions. Although nowadays the recorder of facts, the diagnosticist, does not rank high in science, every theory in Natural History depends especially on the correctness of the facts furnished by the diagnosticist ; when that record lacks correctness the theory based upon it must break down. As an excellent illustration of this we may regard Weismann's theory* of "Phyletic Parallelism in Metamorphic Species," as far as it asserts the existence of an incongruity in the classification of *Lepidoptera* based on larval or based on imaginal characters. The "*Rhopalocera*" are by no means a sharply defined group in the imago state ; neither the erect position of the wing of the resting butterfly and the colour of the wings, nor the clubbed antennae, are characters applying to all "*Rhopalocera*" and exclusively to *Rhopalocera* ; and as there is no single character by which all the *Rhopalocera* are distinguished from all other *Lepidoptera*, we can also not expect that the larvae of *Rhopalocera* form a sharply defined group distinguished as a whole from all other Lepidopterous larvae. The apparent incongruity in the classification according to the larval or imaginal state of "*Bombycidae*" and "*Notodontidae*" again is not due to an incongruent development of larvae and imagines, but to the fact that Lepidopterists have placed in these (and other) families the most heterogeneous things in consequence of an entirely inadequate knowledge of the forms classified.

We learn from this illustration first that diagnostic work is the true basis of evolutionistic theories and hence of the highest importance, and secondly that the record of facts must be exact. Huxley says that the record of facts is not scientific if the facts do not permit of the drawing of general conclusions. In the above case the blame is much more on the side of the systematists who gave the clubbed antennae as distinguishing character of butterflies, than on the side of Weismann who accepted this statement as correct. If, therefore, diagnostic work is intended to meet the claim of furnishing facts from which general conclusions as to evolution (classification, variation, etc.) can safely be drawn, or if a diagnosticist claims to have his work regarded as scientific, it must be well distinguished between the description of the characters of individuals and the statement of an opinion deduced by the diagnosticist from the characters of the individuals ; the record of the characters of individuals, or the statement of facts, ought to precede the statement of the personal conclusion, which perhaps is entirely wrong. In the case of species and lower degrees of divergency diagnosticists mostly lose sight of this ; when we describe a number of individuals as belonging to a new species we present very often to the reader, not the characters of the specimens, but a ready-made conclusion which asserts (1) that the specimens are specifically identical, and (2) that the species varies in colour, markings, structure, and size to such and such an extent. The specific identity and the specific distinctness of the specimens are certainly our deduction, and the variation of the species thus erected is also ours. It is not rarely that one meets with diagnoses of species which give the average of some character of the individuals—for example, the average size—which perhaps is not found in any of the specimens measured, or if found may occur very rarely compared with the greater abundance of large and small individuals.* Most deceptive are those diagnoses which contain statements like these: "Colour brown to black; size 50 to 60 mm.; *habitat* India to New Guinea." In such diagnoses the facts are veiled, and we are easily deceived by taking the diagnosis as being the record of facts, while it is a mere statement of an opinion. The erroneous view expressed by Romanes † that geographical races are less abundant among animals than among plants, and Pagenstecher's view ‡ that moths do not vary to any extent according to locality, are the consequence of such deceptive statements on the side of the diagnosticists. The description of a species or variety, therefore, ought to be a pure statement of facts: as said above, the facts which the diagnosticist deals with are the characters of individuals: a pure statement of facts, with the exclusion of any statement arrived at by reasoning, we should have when the characters of the different individuals were recorded in such a way that from the description it would be plainly visible which characters belong to each single individual. When this is done, the statement of our opinion as to the specific identity of the specimens, the variation and distribution of the species, etc., cannot affect the facts, and, therefore, cannot do much harm, even if our opinion should be wrong. Hence we take it that the description of a species or variety being intended to be a statement of facts, not of conclusions, ought to be the description of one individual to the characters of which the different characters of other individuals are so annexed that a mistake as to which individual a respective character belongs cannot occur. That specimen round which the others are grouped in the description is the *type-specimen* of the description, and as the description is the description of the species or variety (as far as the individuals of the species or variety are known at the time), in the same sense as a figure of an individual is meant to represent the species or variety, that specimen is correctly called *type-specimen* of the species or variety respectively.

---

* Weismann, *Studies in the Theory of Descent*, London. 1882. II. p. 132.

Besides the pure record of morphological facts, the diagnosticist has to draw inferences from the facts: and as the recorder of facts ought to know the facts best, the conclusions the diagnosticist arrives at ought to be generally correct if the method of reasoning is correct. The inferences which concern us here are such as to the specific or non-specific distinctness of groups of individuals, and hence we shall restrict our discussion to this kind of conclusions.

If we received a bird of Paradise with conspicuous ornamental feathers, even if the species were quite unknown to us, we should at once pronounce the specimen to be a *male*, though we know nothing about its having been a physiological *male*; and if the quills of the ornamental feathers were surrounded by a horny sheath, we should conclude that the individual was not yet in full plumage. As Dr. Martin has succeeded in breeding tailed and tailless *females* of *Papilio memnon* from the eggs of one *female* in Sumatra, we must conclude that also in other districts where the two *female* forms occur both can be produced by each of the two. What is found to be true in a number of cases we are bound to conclude to be true in all identity and the specific distinctness of the specimens are certainly our deduction, and the variation of the species thus erected is also ours. It is not rarely that one meets with diagnoses of species which give the average of some character of the individuals—for example, the average size—which perhaps is not found in any of the specimens measured, or if found may occur very rarely compared with the greater abundance of large and small individuals.* Most deceptive are those diagnoses which contain statements like these: "Colour brown to black; size 50 to 60 mm.; *habitat* India to New Guinea." In such diagnoses the facts are veiled, and we are easily deceived by taking the diagnosis as being the record of facts, while it is a mere statement of an opinion. The erroneous view expressed by Romanes † that geographical races are less abundant among animals than among plants, and Pagenstecher's view ‡ that moths do not vary to any extent according to locality, are the consequence of such deceptive statements on the side of the diagnosticists. The description of a species or variety, therefore, ought to be a pure statement of facts; as said above, the facts which the diagnosticist deals with are the characters of individuals: a pure statement of facts, with the exclusion of any statement arrived at by reasoning, we should have when the characters of the different individuals were recorded in such a way that from the description it would be plainly visible which characters belong to each single individual. When this is done, the statement of our opinion as to the specific identity of the specimens, the variation and distribution of the species, etc., cannot affect the facts, and, therefore, cannot do much harm, even if our opinion should be wrong. Hence we take it that the description of a species or variety being intended to be a statement of facts, not of conclusions, ought to be the description of one individual to the characters of which the different characters of other individuals are so annexed that a mistake as to which individual a respective character belongs cannot occur. That specimen round which the others are grouped in the description is the *type-specimen* of the description, and as the description is the description of the species or variety (as far as the individuals of the species or variety are known at the time), in the same sense as a figure of an individual is meant to represent the species or variety, that specimen is correctly called *type-specimen* of the species or variety respectively.

---

* See Bateson & Brindley, *P. Z. S.* 1892, pp. 585 ff.

† *Darwin and After Darwin*, London, II. 1895. p. 209.

‡ *Jahrb. Ver. Nass.* 1896. p. 158.

Besides the pure record of morphological facts, the diagnosticist has to draw inferences from the facts: and as the recorder of facts ought to know the facts best, the conclusions the diagnosticist arrives at ought to be generally correct if the method of reasoning is correct. The inferences which concern us here are such as to the specific or non-specific distinctness of groups of individuals, and hence we shall restrict our discussion to this kind of conclusions.

If we received a bird of Paradise with conspicuous ornamental feathers, even if the species were quite unknown to us, we should at once pronounce the specimen to be a *male*, though we know nothing about its having been a physiological *male*; and if the quills of the ornamental feathers were surrounded by a horny sheath, we should conclude that the individual was not yet in full plumage. As Dr. Martin has succeeded in breeding tailed and tailless *females* of *Papilio memnon* from the eggs of one *female* in Sumatra, we must conclude that also in other districts where the two *female* forms occur both can be produced by each of the two. What is found to be true in a number of cases we are bound to conclude to be true in all similar cases. This inductive method of reasoning may often lead to wrong inferences, as the correctness of the latter depends first on the premiss that there are cases which are really proved to be true, and secondly that the cases which we believe to belong to the same category as those proved are really similar cases.

---

* See Bateson & Brindley, *P. Z. S.* 1892. pp. 585 ff.

† *Darwin and After Darwin*, London, II. 1895. p. 209.

‡ *Jahrb. Ver. Nass.* 1896. p. 158.

If we apply this to our question as to specific or non-specific distinctness, it is evident that the conclusion of the diagnosticist can be correct only under the condition that the specific or non-specific distinctness of some forms is proved by experiment, and that he is so well acquainted with the morphology of the forms in question that he can with great probability of correctness decide whether the required similarity is actual or superficial. If in a given group of forms the specific distinctness of any form is not proved, we have to resort to a proved case in an allied group of forms; of course, the more dissimilar the forms referred to for comparison are, the more it becomes probable that our inference is not correct. In most cases it is, therefore, circumstantial evidence we have to judge from, and, as many an innocent man has been condemned by a competent judge on the ground of circumstantial evidence, we cannot very well expect to be always right in our judgment of the specific value of the differences of forms. Though the special evidence furnished by morphology and biology is to be carefully considered in every single case, there are nevertheless some general arguments which apply to a multitude of cases. The question as to specific identity or non-identity concerns first forms which occupy the same area, or whose areas overlap, and secondly forms which inhabit localities separated from one another by districts that are not inhabited, or not inhabitable, by them.

We have above tried to show that a species can develop into more species only with the help of isolation of the varietal forms. If, therefore, two allied species are found to inhabit the same district, no matter whether the areas are totally or only partly the same, it is obvious that at a former period, when the species in question were not yet so far advanced in divergent development, they must have occupied separate areas. From the fact of cohabitation (in a wide sense) the further inference must necessarily be drawn that the possibility of cohabitation without fusion is due to the forms having become so divergent that they are indifferent to one another. The time which has elapsed since the two forms now living together became specifically different must therefore be much greater than that elapsed since the formation of the geographical representatives of those two species. If comparative anatomy and morphology are of any value as to the judgment of the phylogeny of species, the morphological differences between a species and an ally which branched off at an early period must be greater than the differences between the same species and its younger geographical representative species, and still greater than the differences between the geographical forms of the species. If in a given case we have to decide whether *A* and *B*, which live together, are two different species, or two forms of one species, the morphological characters of *A* compared with those of *B* and the geographical representatives of *B* will have to guide us in our judgment. There are three possibilities resulting from the comparison. First, the morphological differences between *A* and *B* are greater than those between *B* and its representatives; in this case *A* and *B* must be considered specifically distinct, until experiment proves the reverse. Secondly, the morphological differences between *A* and *B* are less great than those between *B* and any one of its representatives; in this case *A* and *B* are specifically identical. Thirdly, the differences between *A* and *B* are equal in morphological value to those between *B* and any one of its representatives;

similar cases. This inductive method of reasoning may often lead to wrong inferences, as the correctness of the latter depends first on the premiss that there are cases which are really proved to be true, and secondly that the cases which we believe to belong to the same category as those proved are really similar cases.

If we apply this to our question as to specific or non-specific distinctness, it is evident that the conclusion of the diagnosticist can be correct only under the condition that the specific or non-specific distinctness of some forms is proved by experiment, and that he is so well acquainted with the morphology of the forms in question that he can with great probability of correctness decide whether the required similarity is actual or superficial. If in a given group of forms the specific distinctness of any form is not proved, we have to resort to a proved case in an allied group of forms; of course, the more dissimilar the forms referred to for comparison are, the more it becomes probable that our inference is not correct. In most cases it is, therefore, circumstantial evidence we have to judge from, and, as many an innocent man has been condemned by a competent judge on the ground of circumstantial evidence, we cannot very well expect to be always right in our judgment of the specific value of the differences of forms. Though the special evidence furnished by morphology and biology is to be carefully considered in every single case, there are nevertheless some general arguments which apply to a multitude of cases. The question as to specific identity or non-identity concerns first forms which occupy the same area, or whose areas overlap, and secondly forms which inhabit localities separated from one another by districts that are not inhabited, or not inhabitable, by them.

We have above tried to show that a species can develop into more species only with the help of isolation of the varietal forms. If, therefore, two allied species are found to inhabit the same district, no matter whether the areas are totally or only partly the same, it is obvious that at a former period, when the species in question were not yet so far advanced in divergent development, they must have occupied separate areas. From the fact of cohabitation (in a wide sense) the further inference must necessarily be drawn that the possibility of cohabitation without fusion is due to the forms having become so divergent that they are indifferent to one another. The time which has elapsed since the two forms now living together became specifically different must therefore be much greater than that elapsed since the formation of the geographical representatives of those two species. If comparative anatomy and morphology are of any value as to the judgment of the phylogeny of species, the morphological differences between a species and an ally which branched off at an early period must be greater than the differences between the same species and its younger geographical representative species, and still greater than the differences between the geographical forms of the species. If in a given case we have to decide whether *A* and *B*, which live together, are two different species, or two forms of one species, the morphological characters of *A* compared with those of *B* and the geographical representatives of *B* will have to guide us in our judgment. There are three possibilities resulting from the comparison. First, the morphological differences between *A* and *B* are greater than those between *B* and its representatives; in this case *A* and *B* must be considered specifically distinct, until experiment proves the reverse. Secondly, the morphological differences between *A* and *B* are less great than those between *B* and any one of its representatives; in this case *A* and *B* are specifically identical. Thirdly, the differences between *A* and *B* are equal in morphological value to those between *B* and any one of its representatives;

in this case *A* has to be put in the same relation to *B* in which that respective representative stands to *B*, *i.e.* it must be considered either as specifically different or as specifically identical with *B*, according to the specific distinctness or non-distinctness of that representative.

The same kind of evidence we may employ when we have to come to a decision as to the specific distinctness of geographically separated forms which are not connected by intergradations. But when that evidence is not conclusive enough, we may have recourse to the evidence furnished by the variation of the forms. We must accept as a general law that forms which are connected by all intergradations, or forms which overlap in characters, are specifically identical; geographical form, agreeing with this law are, therefore, to be accepted as specifically non-distinct. If we now compare the various organs of the species in respect to the effect which the causes of variation have upon them, we shall find that a number of characters are easily affected and show a variation between wide limits, while other characters remain comparatively constant. Organ *a* varies, for example, in species *A*, as far as we know at the time, from ten to a hundred, while organ *b* varies only from thirty to thirty-five. Now if it is proved that in a number of allied species a similar difference in respect to the variability of the organs *a* and *b* takes place, we can with great probability of correctness conclude that a form *B* similar to *A* is specifically distinct from *A* if the character of the organ *b* is far outside the range of variation observed in *A*, and, on the other hand, that *B* is a form of the species *A* if the character of the organ *b* comes within the limits of variation observed in *A*, no matter whether *A* and *B* are very similar or very dissimilar in respect to the variable character of the organ *a*.

As long as the special evidence does not force us to conclude otherwise, the diagnosticist has to go by the following two general rules:—

1. If is found that *A* and *B* stand in a certain relation to one another (sexes, aberrations, seasonal forms, subspecies, species), and that the allied forms *C* and *D* differ from one another in a similar way as *A* does from *B*, *C* and *D* have to be put into the same relation to each other in which *A* stands to *B*.

Illustration.—We know by breeding experiments that in Japan the spring brood of *Papilio sarpedon* is smaller and has a wider band than the summer broods; in North India we find an insect very similar to the Japanese one, and observe that in April and May a form flies which is small and has a wide band, and that later in the year all the specimens belong to another form which is somewhat larger and has a narrower band; as in Japan the smaller and the larger forms are proved to be seasonal forms of one species, we are logically bound to regard also the smaller and the larger forms in India as belonging to the spring and summer broods respectively of one species. A good number of allied *Papilios* show in India the same phenomenon; specimens collected during the first half of the year are smaller and have wider bands than the specimens collected later on: though it has not been proved by rearing that we have here actually to do with spring and summer forms, it would be illogical to regard the spring and summer specimens as specifically distinct.

2. If it is found that *A* and *B* stand in a certain relation to one another, which relation is either proved by experiment or arrived at by general reasoning, a specimen or specimens differing from *A* and *B* in a similar way as *A* does from *B* have to be considered as a third form *C* standing in the same relation to *A* and *B* as *A* does to *B*.

in this case *A* has to be put in the same relation to *B* in which that respective representative stands to *B*, *i.e.* it must be considered either as specifically different or as specifically identical with *B*, according to the specific distinctness or non-distinctness of that representative.

The same kind of evidence we may employ when we have to come to a decision as to the specific distinctness of geographically separated forms which are not connected by intergradations. But when that evidence is not conclusive enough, we may have recourse to the evidence furnished by the variation of the forms. We must accept as a general law that forms which are connected by all intergradations, or forms which overlap in characters, are specifically identical; geographical form, agreeing with this law are, therefore, to be accepted as specifically non-distinct. If we now compare the various organs of the species in respect to the effect which the causes of variation have upon them, we shall find that a number of characters are easily affected and show a variation between wide limits, while other characters remain comparatively constant. Organ *a* varies, for example, in species *A*, as far as we know at the time, from ten to a hundred, while organ *b* varies only from thirty to thirty-five. Now if it is proved that in a number of allied species a similar difference in respect to the variability of the organs *a* and *b* takes place, we can with great probability of correctness conclude that a form *B* similar to *A* is specifically distinct from *A* if the character of the organ *b* is far outside the range of variation observed in *A*, and, on the other hand, that *B* is a form of the species *A* if the character of the organ *b* comes within the limits of variation observed in *A*, no matter whether *A* and *B* are very similar or very dissimilar in respect to the variable character of the organ *a*.

As long as the special evidence does not force us to conclude otherwise, the diagnosticist has to go by the following two general rules:—

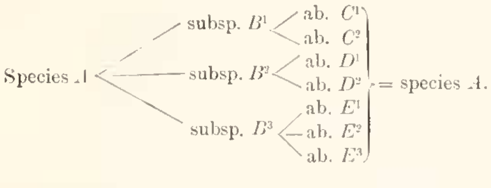
1. If is found that *A* and *B* stand in a certain relation to one another (sexes, aberrations, seasonal forms, subspecies, species), and that the allied forms *C* and *D* differ from one another in a similar way as *A* does from *B*, *C* and *D* have to be put into the same relation to each other in which *A* stands to *B*.

Illustration.—We know by breeding experiments that in Japan the spring brood of *Papilio sarpedon* is smaller and has a wider band than the summer broods; in North India we find an insect very similar to the Japanese one, and observe that in April and May a form flies which is small and has a wide band, and that later in the year all the specimens belong to another form which is somewhat larger and has a narrower band; as in Japan the smaller and the larger forms are proved to be seasonal forms of one species, we are logically bound to regard also the smaller and the larger forms in India as belonging to the spring and summer broods respectively of one species. A good number of allied *Papilios* show in India the same phenomenon; specimens collected during the first half of the year are smaller and have wider bands than the specimens collected later on: though it has not been proved by rearing that we have here actually to do with spring and summer forms, it would be illogical to regard the spring and summer specimens as specifically distinct.

2. If it is found that *A* and *B* stand in a certain relation to one another, which relation is either proved by experiment or arrived at by general reasoning, a specimen or specimens differing from *A* and *B* in a similar way as *A* does from *B* have to be considered as a third form *C* standing in the same relation to *A* and *B* as *A* does to *B*.

Illustration.—The islands of Sambawa, Alor, Wetter, Timor, Letti, the Tenimber Islands, North Australia, and the New Hebrides, are each inhabited by a subspecies of *Papilio canopus*; the subspecies differ from one another in the shape of the hindwing, and in the extent, presence, and partial absence of the wing-markings. Lately Mr. Rothschild received a specimen of *Papilio* from the island of Sumba differing from the Sambawa and the Alor forms of *canopus* in a similar way as these do from one another and from the Timor form, namely in the partial absence and in the extent of the markings. The only logically possible way, accepted by Mr. Rothschild, was to treat the Sumba specimen also as a form of *canopus*.

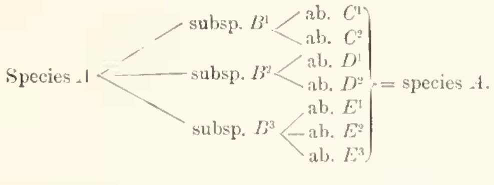
When the evidence leads to the conclusion that the differences exhibited by a number of specimens, or forms represented by specimens, are not specific, it is self-evident that the various forms belong to one species. This species, then, consists of a number of different varieties, every single individual of which, however aberrant it may be, represents the species, and every single peculiarity of any individual is a peculiarity of the species: all the specimens of all the various forms taken together are "the species" as opposed to every other species. The diagnosis of this species, which must not be confounded with the description of the species, is therefore a diagnosis of a sum of varieties; and as a diagnosis is analogous to the definition of a term, it must contain all the distinguishing characters common to all the specimens, and hence must apply to each single specimen. Besides the specific distinguishing characters each variety has one or more characters of its own which form the diagnosis of each respective variety. The discovery of a new variety, which was hitherto unknown on account of the incompleteness of our knowledge, or which has sprung up in consequence of the area of the species having recently become extended (*Pieris rapae* ab. loc. *novangliae*, for example), may necessitate an alteration of the diagnosis of the species to which the new variety belongs. As the forms diagnosticated for the sake of convenience are fixed by a name given to each of them, it is obvious that the only way logically possible to name a species and its subordinate components is to give a name of its own to the species, one to each subspecies as subordinate to the species, and one to each individual aberration as subordinate to the subspecies. Diagrammatically it can be illustrated thus:—



Every individual forms together with other individuals a group characterised by a peculiarity not met with in the rest of the individuals, which, therefore, form another group (or more), termed here *individual aberration* = *ab.* A number of individual aberrations are the components of a subspecies, and a number of subspecies the components of a species. Each specimen will require in this case a specific, a subspecific, and an aberrational name. In many cases, however, the nomenclature will become much simplified by aberrational names being unnecessary, because the individuals do not vary to such an extent within a subspecies that aberrational names are required; the simplification will be still greater when, besides the aberrational names, the subspecific names are not required. In order

Illustration.—The islands of Sambawa, Alor, Wetter, Timor, Letti, the Tenimber Islands, North Australia, and the New Hebrides, are each inhabited by a subspecies of *Papilio canopus*; the subspecies differ from one another in the shape of the hindwing, and in the extent, presence, and partial absence of the wing-markings. Lately Mr. Rothschild received a specimen of *Papilio* from the island of Sumba differing from the Sambawa and the Alor forms of *canopus* in a similar way as these do from one another and from the Timor form, namely in the partial absence and in the extent of the markings. The only logically possible way, accepted by Mr. Rothschild, was to treat the Sumba specimen also as a form of *canopus*.

When the evidence leads to the conclusion that the differences exhibited by a number of specimens, or forms represented by specimens, are not specific, it is self-evident that the various forms belong to one species. This species, then, consists of a number of different varieties, every single individual of which, however aberrant it may be, represents the species, and every single peculiarity of any individual is a peculiarity of the species: all the specimens of all the various forms taken together are "the species" as opposed to every other species. The diagnosis of this species, which must not be confounded with the description of the species, is therefore a diagnosis of a sum of varieties; and as a diagnosis is analogous to the definition of a term, it must contain all the distinguishing characters common to all the specimens, and hence must apply to each single specimen. Besides the specific distinguishing characters each variety has one or more characters of its own which form the diagnosis of each respective variety. The discovery of a new variety, which was hitherto unknown on account of the incompleteness of our knowledge, or which has sprung up in consequence of the area of the species having recently become extended (*Pieris rapae* ab. loc. *novangliae*, for example), may necessitate an alteration of the diagnosis of the species to which the new variety belongs. As the forms diagnosticated for the sake of convenience are fixed by a name given to each of them, it is obvious that the only way logically possible to name a species and its subordinate components is to give a name of its own to the species, one to each subspecies as subordinate to the species, and one to each individual aberration as subordinate to the subspecies. Diagrammatically it can be illustrated thus:—



Every individual forms together with other individuals a group characterised by a peculiarity not met with in the rest of the individuals, which, therefore, form another group (or more), termed here *individual aberration = ab.* A number of individual aberrations are the components of a subspecies, and a number of subspecies the components of a species. Each specimen will require in this case a specific, a subspecific, and an aberrational name. In many cases, however, the nomenclature will become much simplified by aberrational names being unnecessary, because the individuals do not vary to such an extent within a subspecies that aberrational names are required; the simplification will be still greater when, besides the aberrational names, the subspecific names are not required. In order to avoid grave mistakes it is necessary that we insert before the aberrational name some sign to indicate that the name is meant for an aberration. For, in species which do not vary according to locality we often have important individual variation, and therefore have to designate individuals with aberrant characters, besides by the generic name, by a specific and an aberrational name only, thus: *Papilio gambrisius* ab. *abbreviatus*; *P. gambrisius abbreviatus* would have an entirely different and erroneous meaning. The abbreviations employed as a sign may be *ab.* for the usual individual aberration, *ab. loc.* for localised individual aberration, ♂-*ab.* and ♀-*ab.* for aberrations occurring only in one sex, ♀-*f.* for a constantly appearing form of polymorphic species, ♀-*f. loc.* when the form is localised, *gen. vern.* and *gen. aest.* for seasonal forms. In this way the various kinds of individual variation can be distinguished by the special sign employed, which would not be possible if the aberrational name were simply annexed to the subspecific or specific name.

Since the diagnosticist when describing a form very often does not know whether this form will ultimately turn out to be cospecific with other forms, or whether it is actually specifically distinct, and as, further, a great many forms have been diagnosticated as species which now are known to be subspecies (and the reverse), the question arises how the above system of nomenclature must be carried out. For the sake of simplicity we shall take into account solely a species with its subspecies; then we have the following possible cases:—

1. The first diagnosis and description are so general that they apply very well to a certain species A, but do not give any character from which we could see which one of the subspecies (B^1, B^2, B^3) of A the author has had before him. In this case the name given by the author must be kept for the species A, and each subspecies requires another name.

2. The first diagnosis and description apply to two or more forms (but not to all) which are now known to be subspecies of a certain species, and are so general that we do not know whether the author had one or more forms before him. In this case again the first name must be employed for the species, and each subspecies requires another name.

3. The diagnosis applies not to one entire species A, but to one particular subspecies B^1 of A; the other subspecies B^2 and B^3 of A either were not known to the respective author, or their specific identity with B^1 was not recognised by him. B^1 may be the first described of the three forms. Which name must be used for the species A? Illustration: Linné described the Amboina form of a beautiful insect under the name of *Papilio priamus*; we know now that this Amboina form is a subspecies of a species which ranges over nearly the whole of the Papuan region and has developed into several subspecies. Linné's name of *priamus* was given, not to the entire species, but to one particular subspecies, and there is not the least doubt that this name must be kept to designate that particular subspecies. Now, how have we to call the entire species? A short consideration of what a name is meant for and how systematists employ a name will give a satisfactory answer. A diagnosticist describes a species x from a number of individuals; further researches show that the characters in the original description apply only to a certain number of specimens; aberrant specimens are found, and the result is that the original description of the species has to be largely modified; but, in spite of this, the original name is kept for the species. Illustration: Linné's description of *Papilio podalirius* does not apply to certain aberrations which occasionally occur among the

to avoid grave mistakes it is necessary that we insert before the aberrational name some sign to indicate that the name is meant for an aberration. For, in species which do not vary according to locality we often have important individual variation, and therefore have to designate individuals with aberrant characters, besides by the generic name, by a specific and an aberrational name only, thus: *Papilio gambrisius* ab. *abbreviatus*; *P. gambrisius abbreviatus* would have an entirely different and erroneous meaning. The abbreviations employed as a sign may be *ab.* for the usual individual aberration, *ab. loc.* for localised individual aberration, ♂-*ab.* and ♀-*ab.* for aberrations occurring only in one sex, ♀-*f.* for a constantly appearing form of polymorphic species, ♀-*f. loc.* when the form is localised, *gen. vern.* and *gen. aest.* for seasonal forms. In this way the various kinds of individual variation can be distinguished by the special sign employed, which would not be possible if the aberrational name were simply annexed to the subspecific or specific name.

Since the diagnosticist when describing a form very often does not know whether this form will ultimately turn out to be cospecific with other forms, or whether it is actually specifically distinct, and as, further, a great many forms have been diagnosticated as species which now are known to be subspecies (and the reverse), the question arises how the above system of nomenclature must be carried out. For the sake of simplicity we shall take into account solely a species with its subspecies; then we have the following possible cases:—

1. The first diagnosis and description are so general that they apply very well to a certain species A, but do not give any character from which we could see which one of the subspecies (B^1, B^2, B^3) of A the author has had before him. In this case the name given by the author must be kept for the species A, and each subspecies requires another name.

2. The first diagnosis and description apply to two or more forms (but not to all) which are now known to be subspecies of a certain species, and are so general that we do not know whether the author had one or more forms before him. In this case again the first name must be employed for the species, and each subspecies requires another name.

3. The diagnosis applies not to one entire species A, but to one particular subspecies B^1 of A; the other subspecies B^2 and B^3 of A either were not known to the respective author, or their specific identity with B^1 was not recognised by him. B^1 may be the first described of the three forms. Which name must be used for the species A? Illustration: Linné described the Amboina form of a beautiful insect under the name of *Papilio priamus*; we know now that this Amboina form is a subspecies of a species which ranges over nearly the whole of the Papuan region and has developed into several subspecies. Linné's name of *priamus* was given, not to the entire species, but to one particular subspecies, and there is not the least doubt that this name must be kept to designate that particular subspecies. Now, how have we to call the entire species? A short consideration of what a name is meant for and how systematists employ a name will give a satisfactory answer. A diagnosticist describes a species x from a number of individuals; further researches show that the characters in the original description apply only to a certain number of specimens; aberrant specimens are found, and the result is that the original description of the species has to be largely modified; but, in spite of this, the original name is kept for the species. Illustration: Linné's description of *Papilio podalirius* does not apply to certain aberrations which occasionally occur among the

normal specimens : nevertheless we include these aberrations under Linné's name, and thus extend the meaning of the name.

As the number of specimens at the disposal of the author is always comparatively small, a name will, in consequence of further research, always cover a larger field than it did when first applied. If we keep this extension of the meaning of a name in view, it is obvious that the name of a certain form has to include all subsequently discovered forms which are specifically identical with the first form. Just as the name of *Papilio podalirius* comprises the so-called normal as well as the aberrational specimens, the name of *Papilio priamus* comprises the particular subspecies *priamus* described by Linné as well as all the more recently discovered forms called *poseidon*, *euphorion*, *richmondius*, etc., as the following diagram shows:—

$$\textit{Papilio priamus}\begin{cases}\textit{priamus},\\ \textit{poseidon},\\ \textit{euphorion},\\ \text{etc.}\end{cases}$$

That is to say, the first name given to any member of a species is to be taken as the name of the entire species. The consequence is that the name of the species must be repeated when the respective component to which it originally was given is to be designated. Thus it might very often happen that a particular individual aberration had to be called after this pattern : *Papilio polytes polytes* ♀-f. *polytes*. The meaning of this name is exclusive and hence precise, and that is the highest praise we can give to a name : ♀-f. *polytes* shows that the *female* sex of the subspecies *polytes* is polymorphic, ♀-f. *polytes* being co-ordinate to one or some other aberrations of that sex (♀-f. *cyrus*, ♀-f. *romulus*): *polytes* ♀-f. *polytes* means that the particular *female* form was the first described ; *polytes polytes* has again the meaning that the particular subspecies was the first described of all those which belong to the species *polytes*.

A few illustrations will more especially show the convenience of this method of nomenclature. Boucard described one of those beautiful Central-American beetles which belong to the genus *Plusiotis* under the name of *aurora* ; the specimen has remained unique as far as we know, while many individuals have afterwards been found which, though specifically identical with the first-described specimen, differ from the latter very conspicuously in colour, being green instead of aurora-colour. The aurora-coloured individual is apparently a so-called accidental aberration, while the green individuals are the normal (or morphologically typical) ones. According to the old style of nomenclature the two forms would have to stand as *Plusiotis aurora* (accidental aberration) and *Plusiotis aurora* ab. *chrysopedila* (normal form). How absurd this kind of nomenclature is will easily be understood if we take, instead of these beetles, an albinistic specimen and normal individuals of a mammal or bird. Our method treats both forms as forms of one species, *Plusiotis aurora* ab. *aurora* and *Pl. aurora* ab. *chrysopedila*, the species *aurora* thus being composed of a normal form (ab. *chrysopedila*) and an aberrant form (ab. *aurora*).

A European moth of the genus *Hepialus* has developed into two subspecies, one with ♂ and ♀ nearly the same in colour (*hethlandicus*), and the other with ♂ and ♀ very different in colour (*humuli*); the first is said to be phylogenetically the older form, and therefore represents morphologically the typical one of the two ; the first described, however, is the sexually dimorphic form *humuli*, and therefore the typical normal specimens : nevertheless we include these aberrations under Linné's name, and thus extend the meaning of the name.

As the number of specimens at the disposal of the author is always comparatively small, a name will, in consequence of further research, always cover a larger field than it did when first applied. If we keep this extension of the meaning of a name in view, it is obvious that the name of a certain form has to include all subsequently discovered forms which are specifically identical with the first form. Just as the name of *Papilio podalirius* comprises the so-called normal as well as the aberrational specimens, the name of *Papilio priamus* comprises the particular subspecies *priamus* described by Linné as well as all the more recently discovered forms called *poseidon*, *euphorion*, *richmondius*, etc., as the following diagram shows:—

$$\textit{Papilio priamus}\left\{\begin{array}{l}\textit{priamus,}\\ \textit{poseidon,}\\ \textit{euphorion,}\\ \text{etc.}\end{array}\right.$$

That is to say, the first name given to any member of a species is to be taken as the name of the entire species. The consequence is that the name of the species must be repeated when the respective component to which it originally was given is to be designated. Thus it might very often happen that a particular individual aberration had to be called after this pattern : *Papilio polytes polytes* ♀-f. *polytes*. The meaning of this name is exclusive and hence precise, and that is the highest praise we can give to a name : ♀-f. *polytes* shows that the *female* sex of the subspecies *polytes* is polymorphic, ♀-f. *polytes* being co-ordinate to one or some other aberrations of that sex (♀-f. *cyrus*, ♀-f. *romulus*): *polytes* ♀-f. *polytes* means that the particular *female* form was the first described ; *polytes polytes* has again the meaning that the particular subspecies was the first described of all those which belong to the species *polytes*.

A few illustrations will more especially show the convenience of this method of nomenclature. Boucard described one of those beautiful Central-American beetles which belong to the genus *Plusiotis* under the name of *aurora* ; the specimen has remained unique as far as we know, while many individuals have afterwards been found which, though specifically identical with the first-described specimen, differ from the latter very conspicuously in colour, being green instead of aurora-colour. The aurora-coloured individual is apparently a so-called accidental aberration, while the green individuals are the normal (or morphologically typical) ones. According to the old style of nomenclature the two forms would have to stand as *Plusiotis aurora* (accidental aberration) and *Plusiotis aurora* ab. *chrysopedila* (normal form). How absurd this kind of nomenclature is will easily be understood if we take, instead of these beetles, an albinistic specimen and normal individuals of a mammal or bird. Our method treats both forms as forms of one species, *Plusiotis aurora* ab. *aurora* and *Pl. aurora* ab. *chrysopedila*, the species *aurora* thus being composed of a normal form (ab. *chrysopedila*) and an aberrant form (ab. *aurora*).

A European moth of the genus *Hepialus* has developed into two subspecies, one with ♂ and ♀ nearly the same in colour (*hethlandicus*), and the other with ♂ and ♀ very different in colour (*humuli*); the first is said to be phylogenetically the older form, and therefore represents morphologically the typical one of the two ; the first described, however, is the sexually dimorphic form *humuli*, and therefore the typical one in a nomenclatorial sense. Morphology and nomenclature come into contest if we employ the old style of naming the forms, while the contest is entirely avoided by accepting our method, according to which the species *Hepialus humuli* comprises two forms, *Hepialus humuli humuli* and *Hepialus humuli hethlandicus*.

A species of *Pieris* was described by Linné in 1758 as *Pieris napi*, while the Alpine and boreal variety of it, which has a different appearance, received in 1808 the name of *Pieris bryoniae*. From the experiments with this insect carried out by Weismann and others, the inference has been drawn * that *bryoniae* is phylogenetically the older one of the two forms, and that, therefore, the species ought to bear the younger name of *bryoniae* instead of the older name of *napi*. As the meaning of *Pieris napi* var. *bryoniae*, which is the name of the Alpine and boreal butterfly according to the old style of nomenclature, is that *bryoniae* is a variety originated in consequence of the variation of *napi*, an alteration is indeed necessary if the above interpretation of the experiments is correct, and thus evolutionists would have to play havoc with the names of all those numerous species of which a younger form happens to be described first. We have, however, endeavoured to show † that *the species* is represented neither by the white form *napi*, nor by the darker form *bryoniae*, but is composed of *napi* and *bryoniae*; the *species* is not congruent with the *ancestral* form of the recent forms, but is congruent with the sum of the recent forms, and its name is, therefore, independent of the name of that form which is supposed to be phylogenetically the oldest of the component forms. According to our method of nomenclature the name of the *species* in question would be *Pieris napi*, the name of the Alpine and boreal form *P. napi bryoniae*, and that of the form inhabiting the rest of Central and Northern Europe *P. napi napi*. If in theoretical treatises it is necessary to distinguish nomenclatorially the oldest from the younger forms of a species, it could be done by adding (f. prim.) = *forma primigenia*, or some such sign, to the name—*P. napi bryoniae* (f. prim.).

The various points in these introductory notes have been very cursorily dealt with: but we are in hopes that the remarks, in spite of their shortness, will serve to explain our interpretation of the facts of variation we are now going to bring before the reader.

II.—THE VARIATION OF THE GENITAL ARMATURE OF CERTAIN PAPILIOS.

The prehensile organs situated round the orifice of the sexual system of insects have for about fifty years been made use of for diagnostic purposes, and it was, and is, a general belief that the genital armature is of such great constancy in every species that peculiarities exhibited by certain individuals in these internal ectodermal organs, and not found in other individuals which otherwise are very slightly different from those, are of specific value. As we have shown in the introduction that every individual has its individual peculiarities, a slight distinguishing character of an individual, besides the sexual armature, can always be found, and therefore the above opinion leads practically to the assertion that a specimen with some kind of peculiarity in the sexual armature is specifically distinct from the specimens which do not have that peculiarity. On the other hand, one in a nomenclatorial sense. Morphology and nomenclature come into contest if we employ the old style of naming the forms, while the contest is entirely avoided by accepting our method, according to which the species *Hepialus humuli* comprises two forms, *Hepialus humuli humuli* and *Hepialus humuli hethlandicus*.

---

* Weismann, *Studies in the Theory of Descent* I. London, 1882. pp. 61 ff.

† Compare also Lorenz, *Sitz.-Ber. zool. bot. Ges. Wien* 1892. p. 17; Jordan, Nov. Zool. 1895. p. 182; Hartert, *Ibis* 1896. p. 363.

A species of *Pieris* was described by Linné in 1758 as *Pieris napi*, while the Alpine and boreal variety of it, which has a different appearance, received in 1808 the name of *Pieris bryoniae*. From the experiments with this insect carried out by Weismann and others, the inference has been drawn * that *bryoniae* is phylogenetically the older one of the two forms, and that, therefore, the species ought to bear the younger name of *bryoniae* instead of the older name of *napi*. As the meaning of *Pieris napi* var. *bryoniae*, which is the name of the Alpine and boreal butterfly according to the old style of nomenclature, is that *bryoniae* is a variety originated in consequence of the variation of *napi*, an alteration is indeed necessary if the above interpretation of the experiments is correct, and thus evolutionists would have to play havoc with the names of all those numerous species of which a younger form happens to be described first. We have, however, endeavoured to show † that *the species* is represented neither by the white form *napi*, nor by the darker form *bryoniae*, but is composed of *napi* and *bryoniae*; the *species* is not congruent with the *ancestral* form of the recent forms, but is congruent with the sum of the recent forms, and its name is, therefore, independent of the name of that form which is supposed to be phylogenetically the oldest of the component forms. According to our method of nomenclature the name of the *species* in question would be *Pieris napi*, the name of the Alpine and boreal form *P. napi bryoniae*, and that of the form inhabiting the rest of Central and Northern Europe *P. napi napi*. If in theoretical treatises it is necessary to distinguish nomenclatorially the oldest from the younger forms of a species, it could be done by adding (f. prim.) = *forma primigenia*, or some such sign, to the name—*P. napi bryoniae* (f. prim.).

The various points in these introductory notes have been very cursorily dealt with: but we are in hopes that the remarks, in spite of their shortness, will serve to explain our interpretation of the facts of variation we are now going to bring before the reader.

II.—THE VARIATION OF THE GENITAL ARMATURE OF CERTAIN PAPILIOS.

The prehensile organs situated round the orifice of the sexual system of insects have for about fifty years been made use of for diagnostic purposes, and it was, and is, a general belief that the genital armature is of such great constancy in every species that peculiarities exhibited by certain individuals in these internal ectodermal organs, and not found in other individuals which otherwise are very slightly different from those, are of specific value. As we have shown in the introduction that every individual has its individual peculiarities, a slight distinguishing character of an individual, besides the sexual armature, can always be found, and therefore the above opinion leads practically to the assertion that a specimen with some kind of peculiarity in the sexual armature is specifically distinct from the specimens which do not have that peculiarity. On the other hand, comparatively very few authors [*] have given expression to the opinion, not only that there is a certain amount of variability found in those organs, but that one can by no means rely upon them in the judgment of specific distinctness or non-distinctness. During our researches on the Eastern Papilios [†] we came across some striking cases of variability of the copulatory organs which made it evident to us that the above assertion of an extensive variability was not the outcome of superficial research, and this induced the Honourable Walter Rothschild to charge me with investigations in the matter. As Mr. Rothschild knew from the study of the external characters of the Eastern Papilios that a decision about the specific distinctness of these variable insects with some certain degree of correctness could not be arrived at unless one had ascertained with some probability of correctness the limits of individual variation of each form (no matter whether the form was described as species or variety), and hence in order to come as nearly as possible to the knowledge of the limits of variation it was necessary to compare a great many specimens, he liberally put the long series of individuals of his collection at my disposal, and to this the results of our investigations are largely due. It seemed to us that in the first place the aim of our researches had to be to ascertain whether the alleged constancy of the genital armature was, at least in most species, real, especially as compared with the distinguishing characters derived from the wing-pattern. A little consideration, however, showed us that this was scarcely necessary. First, if we accept the statement that every specifically distinct form is to some degree different from the allied forms in the genital armature as being true, it by no means follows that the inverse is correct, namely that forms presenting in the sexual organs some differences from the allied forms are specifically distinct. Hence the proof of the variability of the organs in question would not imply that these organs are useless for diagnostic purposes, though their taxonomic value would certainly be lessened. Secondly, if two or more allied species are different in the sexual organs we have to conclude from the theory of evolution that the present differences are the outcome of divergent development of the allied species from a common ancestral species which itself had the sexual organs either different from all its descendant species, or from all but one; if we concede this, and all followers of Darwin have to do so, it is self-evident that the ancestral species must have been variable in the sexual armature. As, therefore, in the ancestors of our present species the genital armature must be assumed to have been so variable that the variation could lead to specific separation, we cannot but assume *a priori* that in all the species of the present which are in the state of diverging into varieties the genital organs must exhibit not only some variability, but also variation to such an extent that the genital characters of a certain variety could be increased by the factors of evolution and ultimately be transformed into specific characters, unless one tries to avoid these consequences either by abandoning evolution altogether, which would be acceptable, or by maintaining that evolution is not going on during the present epoch, which would be ridiculous.

---

* Weismann, *Studies in the Theory of Descent* I. London, 1882. pp. 61 ff.

† Compare also Lorenz, *Sitz.-Ber. zool. bot. Ges. Wien* 1892. p. 17; Jordan, Nov. Zool. 1895. p. 182; Hartert, *Ibis* 1896. p. 363.

This consideration made it pretty clear to us that the more important part of our investigations would have to be, not to prove the occurrence of variation of the organs in question, but to ascertain the kind of variation, especially to accumulate such facts from which could be seen whether there is individual, comparatively very few authors * have given expression to the opinion, not only that there is a certain amount of variability found in those organs, but that one can by no means rely upon them in the judgment of specific distinctness or non-distinctness. During our researches on the Eastern Papilios † we came across some striking cases of variability of the copulatory organs which made it evident to us that the above assertion of an extensive variability was not the outcome of superficial research, and this induced the Honourable Walter Rothschild to charge me with investigations in the matter. As Mr. Rothschild knew from the study of the external characters of the Eastern Papilios that a decision about the specific distinctness of these variable insects with some certain degree of correctness could not be arrived at unless one had ascertained with some probability of correctness the limits of individual variation of each form (no matter whether the form was described as species or variety), and hence in order to come as nearly as possible to the knowledge of the limits of variation it was necessary to compare a great many specimens, he liberally put the long series of individuals of his collection at my disposal, and to this the results of our investigations are largely due. It seemed to us that in the first place the aim of our researches had to be to ascertain whether the alleged constancy of the genital armature was, at least in most species, real, especially as compared with the distinguishing characters derived from the wing-pattern. A little consideration, however, showed us that this was scarcely necessary. First, if we accept the statement that every specifically distinct form is to some degree different from the allied forms in the genital armature as being true, it by no means follows that the inverse is correct, namely that forms presenting in the sexual organs some differences from the allied forms are specifically distinct. Hence the proof of the variability of the organs in question would not imply that these organs are useless for diagnostic purposes, though their taxonomic value would certainly be lessened. Secondly, if two or more allied species are different in the sexual organs we have to conclude from the theory of evolution that the present differences are the outcome of divergent development of the allied species from a common ancestral species which itself had the sexual organs either different from all its descendant species, or from all but one ; if we concede this, and all followers of Darwin have to do so, it is self-evident that the ancestral species must have been variable in the sexual armature. As, therefore, in the ancestors of our present species the genital armature must be assumed to have been so variable that the variation could lead to specific separation, we cannot but assume *a priori* that in all the species of the present which are in the state of diverging into varieties the genital organs must exhibit not only some variability, but also variation to such an extent that the genital characters of a certain variety could be increased by the factors of evolution and ultimately be transformed into specific characters, unless one tries to avoid these consequences either by abandoning evolution altogether, which would be acceptable, or by maintaining that evolution is not going on during the present epoch, which would be ridiculous.

---

[*] Perez, *Ann. Soc. Ent. Fr.* p. 74 (1894); Edwards, *Canad. Ent.* p. 56 (1894): Kolbe, *Ent. Nachr* p. 133 (1887).

[†] Nov. Zool. p. 269 (1895).

This consideration made it pretty clear to us that the more important part of our investigations would have to be, not to prove the occurrence of variation of the organs in question, but to ascertain the kind of variation, especially to accumulate such facts from which could be seen whether there is individual, seasonal, and geographical polymorphism in the sexual armature. And if such variation be found, the next task would be to compare this variation with that of the external organs, especially with that of the wings, in order to see, first, whether the genital organs and the pattern of the wings were independent of one another in respect to their variation; secondly, whether, in spite of this independence, there are certain kinds of varieties which are characterised by more or less constant peculiarities in the wing-pattern associated with, but not correlated to, peculiarities in the genital armature. As such varieties could easily be mistaken (in fact, have largely been mistaken) for distinct species, and hence would have the appearance of incipient species, and as, further, the divarication of a species can come about only by means of branching into subspecies, we could *a priori* expect to find such a combination of characters in geographical races or subspecies.

---

* Perez, *Ann. Soc. Ent. Fr.* p. 74 (1894) ; Edwards, *Canad. Ent.* p. 56 (1894) : Kolbe, *Ent. Nachr* p. 133 (1887).

† Nov. Zool. p. 269 (1895).

As the present paper stands in close connection with the classificatory investigation on the Papilios we are carrying on, the researches here demonstrated are restricted to that group of insects; and this we deem the more necessary, because the correctness of the results of such work depends to a great extent on the full acquaintance with the various forms dealt with. Though in a monograph of the Papilios all the forms of all the species must be taken into consideration, we have abstained from treating upon all the Palaearctic and Indo-Australian Papilios in this paper for the good reason that, as in every form at least all the more prominent varieties in the genital armature have to be described and figured, the detail of the paper would be so immense that in consequence of the great amount of detail the single facts of variation would be much obscured. Hence we have thought it best to demonstrate the variation of the genital armature on a small number of species which have been so selected that they very well illustrate, first, the amount of variation; secondly, the kind of variation; and thirdly, both the amount and kind of variation within several, morphologically very different, groups of *Papilio*.

As far as we know, systematists have, as regards *Lepidoptera*, only made use of the *male* genital armature for diagnostic purposes. Salvin * mentions the presence of a kind of armature at the orifice of the vagina, but has not succeeded, in consequence of an inadequate method of preparation, in bringing it forward for the purpose of classification. We first came across the vaginal armature when we studied the morphology of the abdomen of the Papilios with a view of discovering characters which could help us in coming to a decision about the extent of the genera into which the Papilios must be classified, and soon found out, on the one side, that the morphology of the abdomen of the *females*, including the vaginal armature, presents excellent generic characters to the systematist (compare Pl. XIX., f. 181, 182), and, on the other side, that the detail of the structure was of the highest taxonomic value as to the delimitation of species. Therefore we have selected a few of the species examined to illustrate the peculiar structure and the variation of the vaginal armature, and the form of the eighth abdominal segment.

A. Male Genital Armature.

The clasping apparatus of the *male* comprises three organs: (1) a dorsal hook called by Gosse *uncus*: (2) the lateral *valves* or *claspers*, bearing on the inner side ridges, teeth, and hooks called *harpe*; and (3) the *scaphium*, which is situated seasonal, and geographical polymorphism in the sexual armature. And if such variation be found, the next task would be to compare this variation with that of the external organs, especially with that of the wings, in order to see, first, whether the genital organs and the pattern of the wings were independent of one another in respect to their variation; secondly, whether, in spite of this independence, there are certain kinds of varieties which are characterised by more or less constant peculiarities in the wing-pattern associated with, but not correlated to, peculiarities in the genital armature. As such varieties could easily be mistaken (in fact, have largely been mistaken) for distinct species, and hence would have the appearance of incipient species, and as, further, the divarication of a species can come about only by means of branching into subspecies, we could *a priori* expect to find such a combination of characters in geographical races or subspecies.

---

* *Biol. Centrali-Amer., Rhop.* II. p. 189 (1890).

As the present paper stands in close connection with the classificatory investigation on the Papilios we are carrying on, the researches here demonstrated are restricted to that group of insects; and this we deem the more necessary, because the correctness of the results of such work depends to a great extent on the full acquaintance with the various forms dealt with. Though in a monograph of the Papilios all the forms of all the species must be taken into consideration, we have abstained from treating upon all the Palaearctic and Indo-Australian Papilios in this paper for the good reason that, as in every form at least all the more prominent varieties in the genital armature have to be described and figured, the detail of the paper would be so immense that in consequence of the great amount of detail the single facts of variation would be much obscured. Hence we have thought it best to demonstrate the variation of the genital armature on a small number of species which have been so selected that they very well illustrate, first, the amount of variation; secondly, the kind of variation; and thirdly, both the amount and kind of variation within several, morphologically very different, groups of *Papilio*.

As far as we know, systematists have, as regards *Lepidoptera*, only made use of the *male* genital armature for diagnostic purposes. Salvin[*] mentions the presence of a kind of armature at the orifice of the vagina, but has not succeeded, in consequence of an inadequate method of preparation, in bringing it forward for the purpose of classification. We first came across the vaginal armature when we studied the morphology of the abdomen of the Papilios with a view of discovering characters which could help us in coming to a decision about the extent of the genera into which the Papilios must be classified, and soon found out, on the one side, that the morphology of the abdomen of the *females*, including the vaginal armature, presents excellent generic characters to the systematist (compare Pl. XIX., f. 181, 182), and, on the other side, that the detail of the structure was of the highest taxonomic value as to the delimitation of species. Therefore we have selected a few of the species examined to illustrate the peculiar structure and the variation of the vaginal armature, and the form of the eighth abdominal segment.

A. Male Genital Armature.

The clasping apparatus of the *male* comprises three organs: (1) a dorsal hook called by Gosse *uncus*: (2) the lateral *valves* or *claspers*, bearing on the inner side ridges, teeth, and hooks called *harpe*; and (3) the *scaphium*, which is situated

---

[*] *Biol. Centrali-Amer.*, *Rhop.* II. p. 189 (1890).

immediately below the anus and above the penis, and becomes visible when the valves are removed. The homology of these organs has been explained by Dr. Peytoureau in his work entitled *Contribution à l'étude de la Morphologie de l'Armure génitale des Insectes*,* and we therefore refer the reader to that work; it is here sufficient to mention that Dr. Peytoureau comes to the result that the *valves* are lateral wings to the *ninth* segment, which itself becomes visible only by dissection, and that the dorsal *uncus* and the ventral *scaphium*, between which the *anus* is found, represent the *anal* or *tenth* segment: the penis, therefore, has its position between the *ninth* and *tenth* segments.

The *uncus*, *scaphium*, and the *valve* with the *harpe* are of classificatory value, and if we intended to explain here the complete morphology of the genital armature of the Papilios we certainly should have to take all three organs as well as the *penis* into account; merely for the sake of simplifying matters we have restricted our notes almost to the *valve* and *harpe*.

The harpe of the Papilios is a fold of the inner sheath of the valve partly raised to ridges, teeth, hooks, rod-like processes, etc., which are sometimes of rather a complicated structure. We have generally given a figure of the harpe and valve as they appear when viewed with the eye perpendicularly above the plane of the valve, while the figures representing the harpe or parts of it are so drawn that the planes of harpe and paper are the same. Very much depends on the position in which the eye is to the harpe, if the comparative study of these organs is to be of any use; a curved or twisted ridge or process appears very different when viewed under a different angle; and hence we have endeavoured to represent the same organ of the various species and subspecies in the same position, so that a comparison of the figures gives an exact idea of the differences in the organs.

1. **Papilio machaon**; † f. 39 to 45.

This species occurs nearly all over the Palaearctic Region, inclusive of China and Japan, and is found also on the Indian side of the Himalayas at higher elevations, as well as in the Nearctic Region. The lines of delimitation between the Old World forms of *P. machaon* are very difficult to draw, in fact cannot be drawn, as the forms overlap in characters. The most remarkable varieties are the summer brood of the Japanese *machaon*, and the subspecies from the interior of Sikkim and the higher parts of Western China. As we shall have to describe and figure the sexual armature of the various forms of *P. machaon* in another paper, we introduce the species here merely because it is the only British representative of the entire group, and therefore will enable the British entomologist to verify our observations.

The *valve* of *P. machaon* is of a triangular shape, and, though somewhat variable in outline according to the individual specimens, does not present any obvious differences in the specimens of the different subspecies.

The *harpe* is a longitudinal fold lying along the ventral margin of the valve; it is distinctly raised and leans somewhat over dorsally. The basal half or so is rounded and simple, whereas the apical half is compressed, with the upper free edge denticulate, so that it resembles the blade of a saw (f. 39—43, ventral view). The

---

* *Revue Biologique du Nord* VII. 1895. The author gives on pp. 13 to 50 a list of works dealing with the abdomen of insects.

† See note on p. 439.

immediately below the anus and above the penis, and becomes visible when the valves are removed. The homology of these organs has been explained by Dr. Peytoureau in his work entitled *Contribution à l'étude de la Morphologie de l'Armure génitale des Insectes*,* and we therefore refer the reader to that work; it is here sufficient to mention that Dr. Peytoureau comes to the result that the *valves* are lateral wings to the *ninth* segment, which itself becomes visible only by dissection, and that the dorsal *uncus* and the ventral *scaphium*, between which the *anus* is found, represent the *anal* or *tenth* segment: the penis, therefore, has its position between the *ninth* and *tenth* segments.

The *uncus*, *scaphium*, and the *valve* with the *harpe* are of classificatory value, and if we intended to explain here the complete morphology of the genital armature of the Papilios we certainly should have to take all three organs as well as the *penis* into account; merely for the sake of simplifying matters we have restricted our notes almost to the *valve* and *harpe*.

The harpe of the Papilios is a fold of the inner sheath of the valve partly raised to ridges, teeth, hooks, rod-like processes, etc., which are sometimes of rather a complicated structure. We have generally given a figure of the harpe and valve as they appear when viewed with the eye perpendicularly above the plane of the valve, while the figures representing the harpe or parts of it are so drawn that the planes of harpe and paper are the same. Very much depends on the position in which the eye is to the harpe, if the comparative study of these organs is to be of any use; a curved or twisted ridge or process appears very different when viewed under a different angle; and hence we have endeavoured to represent the same organ of the various species and subspecies in the same position, so that a comparison of the figures gives an exact idea of the differences in the organs.

1. **Papilio machaon**; † f. 39 to 45.

This species occurs nearly all over the Palaearctic Region, inclusive of China and Japan, and is found also on the Indian side of the Himalayas at higher elevations, as well as in the Nearctic Region. The lines of delimitation between the Old World forms of *P. machaon* are very difficult to draw, in fact cannot be drawn, as the forms overlap in characters. The most remarkable varieties are the summer brood of the Japanese *machaon*, and the subspecies from the interior of Sikkim and the higher parts of Western China. As we shall have to describe and figure the sexual armature of the various forms of *P. machaon* in another paper, we introduce the species here merely because it is the only British representative of the entire group, and therefore will enable the British entomologist to verify our observations.

The *valve* of *P. machaon* is of a triangular shape, and, though somewhat variable in outline according to the individual specimens, does not present any obvious differences in the specimens of the different subspecies.

The *harpe* is a longitudinal fold lying along the ventral margin of the valve; it is distinctly raised and leans somewhat over dorsally. The basal half or so is rounded and simple, whereas the apical half is compressed, with the upper free edge denticulate, so that it resembles the blade of a saw (f. 39—43, ventral view). The basal, rod-like, portion either immediately runs out into the saw (f. 43), or has to curve a little dorsally to join the saw, the latter being a little more dorsal than the former: this variation is independent of locality.

---

* *Revue Biologique du Nord* VII. 1895. The author gives on pp. 13 to 50 a list of works dealing with the abdomen of insects.

† See note on p. 439.

a. *P. machaon flavus* from Great Britain.

The denticulate portion of the harpe is generally longer than in *machaon machaon* from Germany and in *machaon sphyrus* from South Europe and Asia Minor. F. 39, 40, and 41 are taken from three British specimens, and represent the amount of variation found by us in our series. The proportion of the length of the saw to the entire harpe is in the three specimens 19 : 30, 15 : 30, and 13 : 30 ; the variation in the length of the denticulate portion amounts therefore to almost 50 per cent. of the length of the saw figured in f. 141.

The *uncus* of the British specimens (f. 44, dorsal view) is nearly always slenderer than that of the Continental individuals (f. 45), and agrees very well with that of the Japanese subspecies (spring and summer broods).

b. *P. machaon machaon.*

In f. 45 the *uncus* of an individual from Switzerland is represented to show the divergence from f. 44.

c. *P. machaon sphyrus.*

The harpe of this southern subspecies as well as the harpe of *machaon machaon* agrees on the whole with f. 40, but in some specimens from Asia Minor and Palestine the denticulate portion is remarkably short. F. 42 represents an extreme, the proportion of saw to entire harpe being 11 : 30 : the saw is in this individual from Syria more than 70 per cent. shorter than in the British specimen represented by f. 39, an amount of variation which is higher than we anticipated. The harpe of a Palestine specimen, as drawn in f. 43, is abnormal in so far as the saw does rise gradually, not abruptly.

d. *P. machaon hippocrates* from Japan.

Besides the *uncus* mentioned before, we do not see any difference between the genital armature of this remarkable form and the European *machaon*. The spring and summer broods, though so conspicuously different in size and pattern, also do not exhibit, to our knowledge, any distinguishing character in the organs in question.

As the swallow-tails found in the Wicken Fens, near Cambridge, are doubtless one species, the variation of the species in the length of the denticulate portion of the harpe, or, in other words, of the prehensile part of the harpe, amounts to nearly 50 per cent. As further the Syrian specimens do not differ in the wing-pattern so much from British specimens as in Germany and in Syria the individuals of the first brood very often differ from those of the second brood, and as a line of separation between the characters of British and Syrian specimens is altogether absent, we have also to admit that f. 39 and 42 are taken from the same species, *i.e.* that the variation of the prehensile organ amounts to 73 per cent.

Our conclusions are : (1) The genital armature of *machaon* does not afford any characters by which the various geographical races, distinguished especially by differences in the wing-markings, can be constantly differentiated from one another. The harpe of the British form has, however, on the whole, the longest prehensile part, basal, rod-like, portion either immediately runs out into the saw (f. 43), or has to curve a little dorsally to join the saw, the latter being a little more dorsal than the former: this variation is independent of locality.

a. *P. machaon flavus* from Great Britain.

The denticulate portion of the harpe is generally longer than in *machaon machaon* from Germany and in *machaon sphyrus* from South Europe and Asia Minor. F. 39, 40, and 41 are taken from three British specimens, and represent the amount of variation found by us in our series. The proportion of the length of the saw to the entire harpe is in the three specimens 19 : 30, 15 : 30, and 13 : 30 ; the variation in the length of the denticulate portion amounts therefore to almost 50 per cent. of the length of the saw figured in f. 141.

The *uncus* of the British specimens (f. 44, dorsal view) is nearly always slenderer than that of the Continental individuals (f. 45), and agrees very well with that of the Japanese subspecies (spring and summer broods).

b. *P. machaon machaon.*

In f. 45 the *uncus* of an individual from Switzerland is represented to show the divergence from f. 44.

c. *P. machaon sphyrus.*

The harpe of this southern subspecies as well as the harpe of *machaon machaon* agrees on the whole with f. 40, but in some specimens from Asia Minor and Palestine the denticulate portion is remarkably short. F. 42 represents an extreme, the proportion of saw to entire harpe being 11 : 30 : the saw is in this individual from Syria more than 70 per cent. shorter than in the British specimen represented by f. 39, an amount of variation which is higher than we anticipated. The harpe of a Palestine specimen, as drawn in f. 43, is abnormal in so far as the saw does rise gradually, not abruptly.

d. *P. machaon hippocrates* from Japan.

Besides the *uncus* mentioned before, we do not see any difference between the genital armature of this remarkable form and the European *machaon*. The spring and summer broods, though so conspicuously different in size and pattern, also do not exhibit, to our knowledge, any distinguishing character in the organs in question.

As the swallow-tails found in the Wicken Fens, near Cambridge, are doubtless one species, the variation of the species in the length of the denticulate portion of the harpe, or, in other words, of the prehensile part of the harpe, amounts to nearly 50 per cent. As further the Syrian specimens do not differ in the wing-pattern so much from British specimens as in Germany and in Syria the individuals of the first brood very often differ from those of the second brood, and as a line of separation between the characters of British and Syrian specimens is altogether absent, we have also to admit that f. 39 and 42 are taken from the same species, *i.e.* that the variation of the prehensile organ amounts to 73 per cent.

Our conclusions are : (1) The genital armature of *machaon* does not afford any characters by which the various geographical races, distinguished especially by differences in the wing-markings, can be constantly differentiated from one another. The harpe of the British form has, however, on the whole, the longest prehensile part, while the specimens from Syria and Palestine have that denticulated portion on an average shorter than specimens from England, Central Europe, Sikkim, China, and Japan; the *uncus* is thinner in nearly all British and Japanese individuals than in most individuals from the interjacent countries.

(2) The spring and summer broods are not different in the genital armature.

(3) The prehensile portion of the harpe varies considerably in length; the amount of variation is 73 per cent.

2. **Papilio aegeus**: f. 1 to 11.

According to the wing-pattern the species comprises a subspecies inhabiting New Guinea and Aru (*aegeus ormenus*), another found in Australia (*aegeus aegeus*), a third inhabiting the Kei Islands (*aegeus keianus*), a fourth found on the Banda Islands (*aegeus adrastus*), and a fifth is met with in New Britain (*aegeus bismarckianus*).

Of these we could dissect very long series of the first two forms, while the *males* of the three other subspecies we have not examined for want of sufficient material.

P. aegeus ormenus is in both sexes a very variable insect as regards colour, while the Australian form *aegeus aegeus* is rather constant in that respect.

The *valve* (f. 1, seen from above) is of the usual triangular shape; its ventri-apical angle is sometimes more, sometimes less rounded, regardless of locality as well as of wing-pattern.

The *harpe* lies as in *P. machaon* along the ventral edge of the valve, extending from the base to the apex; it is a rather thin blade with the free upper edge sharp, but not conspicuously dentate, bearing only a fine denticulation at the projecting portions, and leans over dorsally. Before the middle it widens out triangularly to form the *submedian projection*, and its free apical portion is raised above the level of the margin of the valve and forms the *apical projection*. The length and form of these two projections vary individually and subspecifically.

a. *P. aegeus ormenus*; f. 1 to 6.

According to the development of the subapical white band of the forewing the *males* belong to three varietal forms: ♂-ab. *ormenus*, with the band complete on upper- and underside; ♂-ab. *pandion*, with the spots of the band partly obliterated; ♂-ab. *othello*, with the band absent. The three forms occur together in the same locality and are connected by all intergradations. The variation of the sexual armature is entirely independent of that of the variation of the band; individuals of ♂-ab. *othello* are different *inter se*, while some of them agree with certain specimens of ♂-ab. *pandion* or ♂-ab. *ormenus*, and so it is with the latter aberrations. The following remarks, therefore, refer to every form of the *male*.

F. 1 is taken from an individual from Dutch New Guinea (coast near the Arfak Mountains); in this perpendicular view the apical projection of the harpe, being more erect than the shorter submedian one, appears to be short. The harpe of the same individual is represented in f. 2: the submedian projection is broad and triangular, and differs obviously from the same projection of f. 3 to 5, which are taken from individuals from the same locality and represent very well the amount of variation we have found in *aegeus ormenus*. In f. 5 the submedian projection is very small, in f. 4 very high, in f. 3 and 4 much slenderer than in f. 2. A specimen (f. 6) from Finschhafen, German New Guinea, has the projection as broad as it is in f. 2, and nearly as high as it is in f. 4. The usual form of the projection met with while the specimens from Syria and Palestine have that denticulated portion on an average shorter than specimens from England, Central Europe, Sikkim, China, and Japan ; the *uncus* is thinner in nearly all British and Japanese individuals than in most individuals from the interjacent countries.

(2) The spring and summer broods are not different in the genital armature.

(3) The prehensile portion of the harpe varies considerably in length ; the amount of variation is 73 per cent.

2. **Papilio aegeus** : f. 1 to 11.

According to the wing-pattern the species comprises a subspecies inhabiting New Guinea and Aru (*aegeus ormenus*), another found in Australia (*aegeus aegeus*), a third inhabiting the Kei Islands (*aegeus keianus*), a fourth found on the Banda Islands (*aegeus adrastus*), and a fifth is met with in New Britain (*aegeus bismarckianus*).

Of these we could dissect very long series of the first two forms, while the *males* of the three other subspecies we have not examined for want of sufficient material.

P. aegeus ormenus is in both sexes a very variable insect as regards colour, while the Australian form *aegeus aegeus* is rather constant in that respect.

The *valve* (f. 1, seen from above) is of the usual triangular shape ; its ventri-apical angle is sometimes more, sometimes less rounded, regardless of locality as well as of wing-pattern.

The *harpe* lies as in *P. machaon* along the ventral edge of the valve, extending from the base to the apex ; it is a rather thin blade with the free upper edge sharp, but not conspicuously dentate, bearing only a fine denticulation at the projecting portions, and leans over dorsally. Before the middle it widens out triangularly to form the *submedian projection*, and its free apical portion is raised above the level of the margin of the valve and forms the *apical projection*. The length and form of these two projections vary individually and subspecifically.

a. *P. aegeus ormenus*; f. 1 to 6.

According to the development of the subapical white band of the forewing the *males* belong to three varietal forms : ♂-ab. *ormenus*, with the band complete on upper- and underside ; ♂-ab. *pandion*, with the spots of the band partly obliterated ; ♂-ab. *othello*, with the band absent. The three forms occur together in the same locality and are connected by all intergradations. The variation of the sexual armature is entirely independent of that of the variation of the band ; individuals of ♂-ab. *othello* are different *inter se*, while some of them agree with certain specimens of ♂-ab. *pandion* or ♂-ab. *ormenus*, and so it is with the latter aberrations. The following remarks, therefore, refer to every form of the *male*.

F. 1 is taken from an individual from Dutch New Guinea (coast near the Arfak Mountains) ; in this perpendicular view the apical projection of the harpe, being more erect than the shorter submedian one, appears to be short. The harpe of the same individual is represented in f. 2 ; the submedian projection is broad and triangular, and differs obviously from the same projection of f. 3 to 5, which are taken from individuals from the same locality and represent very well the amount of variation we have found in *aegeus ormenus*. In f. 5 the submedian projection is very small, in f. 4 very high, in f. 3 and 4 much slenderer than in f. 2. A specimen (f. 6) from Finschhafen, German New Guinea, has the projection as broad as it is in f. 2, and nearly as high as it is in f. 4. The usual form of the projection met with in most examples from all parts of New Guinea is that of f. 2. The length of the projection varies about from 1 : 2.

The free apical projection of the harpe varies in a similar way in outline and height, as will be seen by comparing f. 2 to 6; the extremes which came under our notice are shown in f. 4 and 5, the length varying about from 2 : 3. The normal size of the apical projection is that of f. 2.

The specimens from British New Guinea, the D'Entrecasteaux Islands, and Woodlark Island have in the harpes no character by which we could distinguish them from the individuals from Northern New Guinea.

b. *P. aegeus aegeus* from Queensland and New South Wales; f. 7 to 11.

Though the Australian form of *aegeus* is in respect to the wing-pattern very constant as compared with *aegeus ormenus*, the variation in the genital armature is just as great as in the New Guinean subspecies. The *male* corresponds in the pattern of the forewing to *aegeus ormenus* ♂-ab. *ormenus*.

The commonest forms of the submedian projection met with are shown in f. 8 and 11; on the whole, the basal edge of the projection is more vertical than in *aegeus ormenus*, but this does not apply to every specimen; the character is especially often obvious in the individuals from New South Wales and Southern Queensland. The apical projection is in a few examples a little higher than in *aegeus ormenus*. F. 7 and 8 are taken from two specimens from Cairns, North Queensland; f. 9 represents an individual from Cedar Bay, thirty miles south of Cooktown; f. 10, with an abnormally high and slender submedian projection, is taken from a Queensland individual without exact locality, while f. 11 represents a New South Wales individual. The variation in the length of the submedian projection is in this selected series not so great as in f. 2 to 6, as we did not find an individual in which the submedian projection was as feebly developed as in f. 5.

The importance of the differences exhibited in f. 2 to 11 will at once become obvious when we compare the harpes of the two nearest allied species.

3. Papilio inopinatus; f. 12.

P. aegeus is on the Tenimber Islands represented by an insect which is comparatively very constant in external characters, and is in colour and pattern always separated from *P. aegeus* by a wide gap. Though the absence of intermediate specimens is not a proof that the Tenimber insect named *inopinatus* is specifically distinct from *P. aegeus*, we have to treat *inopinatus* as a species for the following reasons: the external differences between *inopinatus* and *aegeus* are greater than, or as great as, the differences between the relative forms which are regarded as distinct species; if *lowi* and *mayo* are kept separate from *memnon—rumanzovius*, *deiphontes*, and *deipylus* as distinct from *deiphobus—gambrisius* specifically separate from *aegeus*, then *inopinatus* is likewise to be treated as a distinct species. Further, the variation within the *male* sex of *P. aegeus* from New Guinea, Australia, Aru, Kei, and Banda Islands takes place between such limits that the difference between the extremes is not so great as that between *aegeus* and *inopinatus*; the same applies to the variation of that *female* form of *ormenus* which corresponds to the *female* of *inopinatus*.

Thus we think it fairly safe to consider *inopinatus* specifically distinct. The evidence is to some extent corroborated by the difference exhibited by the harpe. We in most examples from all parts of New Guinea is that of f. 2. The length of the projection varies about from 1 : 2.

The free apical projection of the harpe varies in a similar way in outline and height, as will be seen by comparing f. 2 to 6; the extremes which came under our notice are shown in f. 4 and 5, the length varying about from 2 : 3. The normal size of the apical projection is that of f. 2.

The specimens from British New Guinea, the D'Entrecasteaux Islands, and Woodlark Island have in the harpes no character by which we could distinguish them from the individuals from Northern New Guinea.

b. *P. aegeus aegeus* from Queensland and New South Wales; f. 7 to 11.

Though the Australian form of *aegeus* is in respect to the wing-pattern very constant as compared with *aegeus ormenus*, the variation in the genital armature is just as great as in the New Guinean subspecies. The *male* corresponds in the pattern of the forewing to *aegeus ormenus* ♂-ab. *ormenus*.

The commonest forms of the submedian projection met with are shown in f. 8 and 11; on the whole, the basal edge of the projection is more vertical than in *aegeus ormenus*, but this does not apply to every specimen; the character is especially often obvious in the individuals from New South Wales and Southern Queensland. The apical projection is in a few examples a little higher than in *aegeus ormenus*. F. 7 and 8 are taken from two specimens from Cairns, North Queensland; f. 9 represents an individual from Cedar Bay, thirty miles south of Cooktown; f. 10, with an abnormally high and slender submedian projection, is taken from a Queensland individual without exact locality, while f. 11 represents a New South Wales individual. The variation in the length of the submedian projection is in this selected series not so great as in f. 2 to 6, as we did not find an individual in which the submedian projection was as feebly developed as in f. 5.

The importance of the differences exhibited in f. 2 to 11 will at once become obvious when we compare the harpes of the two nearest allied species.

3. **Papilio inopinatus**; f. 12.

P. aegeus is on the Tenimber Islands represented by an insect which is comparatively very constant in external characters, and is in colour and pattern always separated from *P. aegeus* by a wide gap. Though the absence of intermediate specimens is not a proof that the Tenimber insect named *inopinatus* is specifically distinct from *P. aegeus*, we have to treat *inopinatus* as a species for the following reasons: the external differences between *inopinatus* and *aegeus* are greater than, or as great as, the differences between the relative forms which are regarded as distinct species; if *lowi* and *mayo* are kept separate from *memnon—rumanzovius*, *deiphontes*, and *deipylus* as distinct from *deiphobus—gambrisius* specifically separate from *aegeus*, then *inopinatus* is likewise to be treated as a distinct species. Further, the variation within the *male* sex of *P. aegeus* from New Guinea, Australia, Aru, Kei, and Banda Islands takes place between such limits that the difference between the extremes is not so great as that between *aegeus* and *inopinatus*; the same applies to the variation of that *female* form of *ormenus* which corresponds to the *female* of *inopinatus*.

Thus we think it fairly safe to consider *inopinatus* specifically distinct. The evidence is to some extent corroborated by the difference exhibited by the harpe. We have examined only a few individuals, all of which have the median thin portion of the harpe (f. 12) longer than it is in *aegeus*, especially than we found it to be in *aegeus ormenus*; the submedian projection is broad and low, and the apical projection is likewise shorter than in *aegeus*. A comparison of f. 2 to 11 with 12 evidently shows, however, that the distinguishing points in the harpe of *inopinatus* are of much less weight in the judgment of the specific distinctness of the insect than the external features; the difference between f. 4 and 5 and f. 8 and 11 is far greater than that between f. 12 (*inopinatus*) and 8 or 3 (*aegeus*).

4. **Papilio tydeus**; f. 13 to 16.

This is the representative species of *aegeus* on the Northern Moluccas; the same reasons which induce us to treat *inopinatus* as specifically distinct apply also to this insect. The external differences from *aegeus* are in *tydeus* not quite so great as in *inopinatus*; in opposition to this the harpe of *tydeus* differs much more widely from that of *aegeus*. The clasper or valve of *tydeus* (f. 16) is larger than that of *aegeus*, and the harpe therefore longer. The submedian and apical projections of the harpe are more bent over dorsally, as will be seen by comparing f. 1 and 16. The submedian projection is broad and high, and the apical one is conspicuously higher and more erect than in the allies.

We have examined four individuals from Halmaheira and three from Batjan; there is no localised difference in the harpe of *tydeus*. F. 13, 14, and 16 are taken from Halmaheira individuals; f. 15 represents the harpe of one of the Batjan specimens. The variation in the form and length of the projections is obvious; the apical projection in f. 15 is almost half as broad again as that in f. 14.

The facts here illustrated are as follows:—

(1) The variation of the pattern of the wings of *P. aegeus ormenus* is entirely independent of the variation of the harpe.

(2) The difference in the harpes of *aegeus ormenus* and *aegeus aegeus* is very slight and applies only to scarcely half of the number of specimens examined.

(3) *P. inopinatus*, though in external characters very different from *aegeus*, exhibits in the harpe only a slight, but according to the specimens examined rather constant, difference from *aegeus*.

(4) *P. tydeus*, which is in colour and pattern separated from *aegeus* by a less wide gap, has the harpe in all the specimens examined conspicuously different from that of *aegeus* and *inopinatus*.

(5) If we take the length of the harpe = 100, the projections measured from the plane of the valve to the tip of the projections vary in length as follows:—

P. aegeus: submedian projection from 18 to 33; apical projection from 33 to 45.
P. inopinatus ,, ,, ,, 18 ; ,, ,, ,, 32.
P. tydeus ,, ,, ,, 30 to 33; ,, ,, ,, 51 to 63.

Or, in *aegeus* the variation of the submedian projection amounts to 56 per cent. of the length of longest submedian projection observed, while the variation of the apical projection is 27 per cent.

(6) *P. aegeus* and *tydeus* differ somewhat in the size and outline of the valve.

have examined only a few individuals, all of which have the median thin portion of the harpe (f. 12) longer than it is in *aegeus*, especially than we found it to be in *aegeus ormenus*; the submedian projection is broad and low, and the apical projection is likewise shorter than in *aegeus*. A comparison of f. 2 to 11 with 12 evidently shows, however, that the distinguishing points in the harpe of *inopinatus* are of much less weight in the judgment of the specific distinctness of the insect than the external features; the difference between f. 4 and 5 and f. 8 and 11 is far greater than that between f. 12 (*inopinatus*) and 8 or 3 (*aegeus*).

4. **Papilio tydeus**; f. 13 to 16.

This is the representative species of *aegeus* on the Northern Moluccas; the same reasons which induce us to treat *inopinatus* as specifically distinct apply also to this insect. The external differences from *aegeus* are in *tydeus* not quite so great as in *inopinatus*; in opposition to this the harpe of *tydeus* differs much more widely from that of *aegeus*. The clasper or valve of *tydeus* (f. 16) is larger than that of *aegeus*, and the harpe therefore longer. The submedian and apical projections of the harpe are more bent over dorsally, as will be seen by comparing f. 1 and 16. The submedian projection is broad and high, and the apical one is conspicuously higher and more erect than in the allies.

We have examined four individuals from Halmaheira and three from Batjan; there is no localised difference in the harpe of *tydeus*. F. 13, 14, and 16 are taken from Halmaheira individuals; f. 15 represents the harpe of one of the Batjan specimens. The variation in the form and length of the projections is obvious; the apical projection in f. 15 is almost half as broad again as that in f. 14.

The facts here illustrated are as follows :—

(1) The variation of the pattern of the wings of *P. aegeus ormenus* is entirely independent of the variation of the harpe.

(2) The difference in the harpes of *aegeus ormenus* and *aegeus aegeus* is very slight and applies only to scarcely half of the number of specimens examined.

(3) *P. inopinatus*, though in external characters very different from *aegeus*, exhibits in the harpe only a slight, but according to the specimens examined rather constant, difference from *aegeus*.

(4) *P. tydeus*, which is in colour and pattern separated from *aegeus* by a less wide gap, has the harpe in all the specimens examined conspicuously different from that of *aegeus* and *inopinatus*.

(5) If we take the length of the harpe = 100, the projections measured from the plane of the valve to the tip of the projections vary in length as follows :—

P. aegeus: submedian projection from 18 to 33; apical projection from 33 to 45.
P. inopinatus ,, ,, ,, 18 ; ,, ,, ,, 32.
P. tydeus ,, ,, ,, 30 to 33; ,, ,, ,, 51 to 63.

Or, in *aegeus* the variation of the submedian projection amounts to 56 per cent. of the length of longest submedian projection observed, while the variation of the apical projection is 27 per cent.

(6) *P. aegeus* and *tydeus* differ somewhat in the size and outline of the valve.

5. Papilio polytes ; f. 17 to 37.

The *male* sex of this insect is in the pattern of the wing not very variable, while the *female* exhibits a very great amount of individual and local variation. The species ranges in a good number of subspecies over the Indian and Malayan Subregions, and goes as far as the Moluccas; in New Guinea, the Aru Islands, Queensland, and the islands farther east it is represented by *P. ambrax* and *P. phestus* respectively.

The *valve* is more or less triangular (f. 17 and 31), and varies individually. The *harpe* has the same position as in *P. aegeus*; it is a ventral longitudinal fold; the basal half (or so) is stick-like, while the apical portion is abruptly raised into a thin blade, which leans over dorsally so that its ventral surface is visible when the valve is viewed with the eye above the plane of the valve (as in f. 17 and 31); the harpe thus has the appearance of a hatchet; the upper free edge of the blade is very finely denticulate; the tip of the blade projects free for a short distance, and is somewhat curved dorsally, often forming a blunt hook. The outline of the harpe varies according to locality and to the individual specimen.

a. *P. polytes polytes* from N.W. India to Malacca, Natuna Islands, Tonkin; f. 17 to 26.

The blade of the harpe is highest near its basal (subperpendicular) edge, where it is slightly angulate : a second, more distinct, angle is formed just before the edge slopes down towards the apex of the harpe. The apex is scarcely produced or very slightly so. The degree of variation found by us in the specimens from Continental India is represented by f. 18 to 21.

The form of the harpe as shown in f. 18 is that found in most specimens ; the figure is taken from a Kumaon individual (caught in June 1893). The blade of the harpe of the individual from Bankipore (captured March 20th, 1893) (f. 19) is much less steep basally than usual, its dorsal edge being much reduced in length ; the two angles are conspicuous. The two Burmese (Bassein) examples from which f. 20 and 21 are drawn are especially remarkable for the development of the free apical projection.

In external features *P. polytes* from the Natuna Islands (between Malacca and Borneo) forms a transition from *polytes polytes* to *polytes theseus*. From a long series of individuals examined (captured by A. Everett in September and October 1893) the three most different harpes are here figured (f. 24, 25, 26); the blade agrees very well in shape with that of Indian individuals. The thin carina running from the upper edge of the handle of the harpe along the base of the blade varies from being absent to being well marked.

b. *P. polytes borealis* from China.

All the specimens examined agree in the harpes with *polytes polytes*. The individuals of the interesting variety *P. polytes borealis* ♂-ab. *thibetanus*, in which the white discal markings of the hindwing are partly obliterated, also do not exhibit any peculiarity in the genital armature.

As said in Mr. Rothschild's Revision of the Eastern Papilios, the specimens of *P. polytes* from the Loo Choo Islands (south of Japan) stand intermediate in pattern between *P. polytes borealis* and the Malayan *P. polytes theseus*. The harpe of the Loo Choo *polytes* is in so far remarkable that it differs from the harpe of *polytes*

5. Papilio polytes; f. 17 to 37.

The *male* sex of this insect is in the pattern of the wing not very variable, while the *female* exhibits a very great amount of individual and local variation. The species ranges in a good number of subspecies over the Indian and Malayan Subregions, and goes as far as the Moluccas; in New Guinea, the Aru Islands, Queensland, and the islands farther east it is represented by *P. ambrax* and *P. phestus* respectively.

The *valve* is more or less triangular (f. 17 and 31), and varies individually. The *harpe* has the same position as in *P. aegeus*; it is a ventral longitudinal fold; the basal half (or so) is stick-like, while the apical portion is abruptly raised into a thin blade, which leans over dorsally so that its ventral surface is visible when the valve is viewed with the eye above the plane of the valve (as in f. 17 and 31); the harpe thus has the appearance of a hatchet; the upper free edge of the blade is very finely denticulate; the tip of the blade projects free for a short distance, and is somewhat curved dorsally, often forming a blunt hook. The outline of the harpe varies according to locality and to the individual specimen.

a. *P. polytes polytes* from N.W. India to Malacca, Natuna Islands, Tonkin; f. 17 to 26.

The blade of the harpe is highest near its basal (subperpendicular) edge, where it is slightly angulate: a second, more distinct, angle is formed just before the edge slopes down towards the apex of the harpe. The apex is scarcely produced or very slightly so. The degree of variation found by us in the specimens from Continental India is represented by f. 18 to 21.

The form of the harpe as shown in f. 18 is that found in most specimens; the figure is taken from a Kumaon individual (caught in June 1893). The blade of the harpe of the individual from Bankipore (captured March 20th, 1893) (f. 19) is much less steep basally than usual, its dorsal edge being much reduced in length; the two angles are conspicuous. The two Burmese (Bassein) examples from which f. 20 and 21 are drawn are especially remarkable for the development of the free apical projection.

In external features *P. polytes* from the Natuna Islands (between Malacca and Borneo) forms a transition from *polytes polytes* to *polytes theseus*. From a long series of individuals examined (captured by A. Everett in September and October 1893) the three most different harpes are here figured (f. 24, 25, 26); the blade agrees very well in shape with that of Indian individuals. The thin carina running from the upper edge of the handle of the harpe along the base of the blade varies from being absent to being well marked.

b. *P. polytes borealis* from China.

All the specimens examined agree in the harpes with *polytes polytes*. The individuals of the interesting variety *P. polytes borealis* ♂-ab. *thibetanus*, in which the white discal markings of the hindwing are partly obliterated, also do not exhibit any peculiarity in the genital armature.

As said in Mr. Rothschild's Revision of the Eastern Papilios, the specimens of *P. polytes* from the Loo Choo Islands (south of Japan) stand intermediate in pattern between *P. polytes borealis* and the Malayan *P. polytes theseus*. The harpe of the Loo Choo *polytes* is in so far remarkable that it differs from the harpe of *polytes*

polytes and *polytes theseus* in being (in individuals of equal size) larger (f. 22 and 23); the angles of the blade are less prominent than in *polytes polytes*, by which character it leads over to *P. polytes theseus* (f. 28).

c. *P. polytes nikobarus* from the Nicobars and Andamans; f. 27.

We have now received more material from these islands, and find that *polytes nikobarus* can very well be kept separate from *polytes polytes*, as the greater proportion of the specimens from the Andaman and Nicobar Islands are somewhat different from *polytes polytes*. The harpe confirms this opinion: the outline of its blade is more rounded (f. 27), not exhibiting the two angles found in *polytes polytes* (f. 18), and resembles somewhat that of *P. polytes theseus* from Java (f. 29), except in the apex being obviously truncate.

d. *P. polytes theseus* from the larger and lesser Sunda Islands; f. 28 to 30.

This subspecies differs in the *male* from *P. polytes polytes* in being generally smaller and in having the tail to the hindwing more or less obliterated. The harpe of *P. polytes theseus* is distinguished from that of *polytes polytes* by being in the blade absolutely longer, less raised, much more evenly rounded, and by the apex being more pointed.

Sumatra and Borneo individuals have the blade shorter and higher than Java examples, and hence lead over to *polytes polytes*; f. 28 is taken from a small example from the Kina Balu (North Borneo). Timor specimens agree generally with the Javan individuals in the form of the harpe; f. 30, however, is aberrant in having the second angle of the edge of the blade faintly marked and the apex distinctly truncate in a ventral view.

e. *P. polytes alcindor* from Celebes and Saleyer; f. 34.

The *female* of this subspecies is very aberrant, the *male* much less so. The *male* has one character in common with *P. polytes polytes* and *P. polytes theseus*, namely the presence of blue scales on the underside of the hindwing outside the macular white band, which scales are absent from the subspecies flying on the Philippine and Moluccan Islands. So insignificant as this character is, it becomes interesting when we see that the harpe of *polytes alcindor* (f. 34) comes closer in outline to that of *polytes polytes* (compare f. 25) than to that of *polytes alphenor* from the Sulla Islands (f. 33) or from the Philippines (f. 32). We observe, however, that the tip of harpe of *polytes alcindor* (f. 34), though short, is visibly curved upwards in a similar way as in *polytes alphenor*.

f. *P. polytes perversus* from the islands of Sangir and Talaut; f. 35.

In external features this form combines to a certain extent in the *male* the characters of *polytes alcindor* (Celebes) and *polytes nicanor* (Halmaheira). The harpe comes nearest to that of *alcindor*; has the tip, however, a little more hook-shaped.

g. *P. polytes alphenor* from the Philippine Islands (inclusive of Palawan), the Sulla Islands, and the Southern Moluccas; f. 31 to 33.

The *males* from these various islands agree very well with one another in external characters; the polymorphic *females*, however, are partly different according to locality, thus showing that the insect is on the way to develop into several local races. The harpes of the *males* are, according to locality, slightly different.

polytes and *polytes theseus* in being (in individuals of equal size) larger (f. 22 and 23); the angles of the blade are less prominent than in *polytes polytes*, by which character it leads over to *P. polytes theseus* (f. 28).

c. *P. polytes nikobarus* from the Nicobars and Andamans; f. 27.

We have now received more material from these islands, and find that *polytes nikobarus* can very well be kept separate from *polytes polytes*, as the greater proportion of the specimens from the Andaman and Nicobar Islands are somewhat different from *polytes polytes*. The harpe confirms this opinion; the outline of its blade is more rounded (f. 27), not exhibiting the two angles found in *polytes polytes* (f. 18), and resembles somewhat that of *P. polytes theseus* from Java (f. 29), except in the apex being obviously truncate.

d. *P. polytes theseus* from the larger and lesser Sunda Islands; f. 28 to 30.

This subspecies differs in the *male* from *P. polytes polytes* in being generally smaller and in having the tail to the hindwing more or less obliterated. The harpe of *P. polytes theseus* is distinguished from that of *polytes polytes* by being in the blade absolutely longer, less raised, much more evenly rounded, and by the apex being more pointed.

Sumatra and Borneo individuals have the blade shorter and higher than Java examples, and hence lead over to *polytes polytes*; f. 28 is taken from a small example from the Kina Balu (North Borneo). Timor specimens agree generally with the Javan individuals in the form of the harpe; f. 30, however, is aberrant in having the second angle of the edge of the blade faintly marked and the apex distinctly truncate in a ventral view.

e. *P. polytes alcindor* from Celebes and Saleyer; f. 34.

The *female* of this subspecies is very aberrant, the *male* much less so. The *male* has one character in common with *P. polytes polytes* and *P. polytes theseus*, namely the presence of blue scales on the underside of the hindwing outside the macular white band, which scales are absent from the subspecies flying on the Philippine and Moluccan Islands. So insignificant as this character is, it becomes interesting when we see that the harpe of *polytes alcindor* (f. 34) comes closer in outline to that of *polytes polytes* (compare f. 25) than to that of *polytes alphenor* from the Sulla Islands (f. 33) or from the Philippines (f. 32). We observe, however, that the tip of harpe of *polytes alcindor* (f. 34), though short, is visibly curved upwards in a similar way as in *polytes alphenor*.

f. *P. polytes perversus* from the islands of Sangir and Talaut; f. 35.

In external features this form combines to a certain extent in the *male* the characters of *polytes alcindor* (Celebes) and *polytes nicanor* (Halmaheira). The harpe comes nearest to that of *alcindor*; has the tip, however, a little more hook-shaped.

g. *P. polytes alphenor* from the Philippine Islands (inclusive of Palawan), the Sulla Islands, and the Southern Moluccas; f. 31 to 33.

The *males* from these various islands agree very well with one another in external characters; the polymorphic *females*, however, are partly different according to locality, thus showing that the insect is on the way to develop into several local races. The harpes of the *males* are, according to locality, slightly different.

In all the specimens examined the blade of the harpe is conspicuously longer and slenderer than in all the other subspecies of *P. polytes*, and reaches close to the apical margin of the valve (f. 31, taken from a Mindoro example); the narrow apical portion is especially long, and often rather strongly hook-shaped, the hook projecting above the level of the raised ventri-apical edge of the valve.

The harpe of the average example from the Philippines is represented in f. 32; it has a very different appearance from the harpe represented in f. 18 to 26, while the difference between f. 32 and 29 is less conspicuous; the variation of the Philippine examples takes place in such a direction that some individuals approach f. 35.

Of the *males* from the Sulla Islands Mr. Rothschild says that they are not exactly identical with the Philippine *alphenor* in wing-pattern, but approach a little *P. polytes perversus*. The harpes of the Sulla *males* (f. 33) are, on the contrary, still slenderer than in Philippine *alphenor*, thus indicating that a relationship in wing-pattern is not necessarily corroborated by the development of the genital armature.

From the Southern Moluccas we had unfortunately only one individual at our disposal ; the harpe of this specimen is shaped nearly as in *polytes perversus* (f. 35).

In the harpes, therefore, the *males* of *alphenor* from the three localities (Philippine Islands, Sulla Islands, and Southern Moluccas) are fairly well distinguishable, though there is no distinct line of separation.

h. *P. polytes nicanor* from Halmaheira and Batjan; f. 36.

The blade of the harpe is much higher than in *polytes alphenor*, and in this respect *nicanor* comes nearest to the Indian *polytes polytes*; the apex of the harpe is produced, nearly as in *alphenor*. F. 36 is taken from a Halmaheira individual.

6. **Papilio ambrax**; f. 37 and 38.

The outline of the valve (f. 38) of this species varies individually. The harpe is generally formed as in f. 37, but is sometimes somewhat slenderer and at the apex less hooked.

We merely give the two figures of the valve and harpe of an *ambrax* individual (from German New Guinea) in order to enable the reader to compare them with f. 18 to 36. The differences between f. 37 (*ambrax*) and 36 or 34 (*polytes*), belonging to two species, are not so conspicuous as the divergency exhibited by various harpes within the species *polytes*.

The facts of variation observed in *P. polytes* are as follows :—

(1) The valve is variable in the individual specimens, but does not exhibit in the specimens examined any obvious variation according to locality.

(2) The conspicuous individual aberration *P. polytes borealis* ♂-ab. *thibetanus* has no peculiarity in the genital armature.

(3) The individual variation in the blade of the harpe of the individuals from India is such (f. 18 and 19) that the extremes stand further apart than many individuals of *polytes polytes* do from many individuals of *polytes theseus*.

(4) The harpe of *polytes theseus* from Java and the lesser Sunda Islands is well distinguished from that of the Indian *polytes polytes*, but there is no parting line on account of the intermediate form of the harpe of *polytes theseus* from Borneo and Sumatra.

In all the specimens examined the blade of the harpe is conspicuously longer and slenderer than in all the other subspecies of *P. polytes*, and reaches close to the apical margin of the valve (f. 31, taken from a Mindoro example); the narrow apical portion is especially long, and often rather strongly hook-shaped, the hook projecting above the level of the raised ventri-apical edge of the valve.

The harpe of the average example from the Philippines is represented in f. 32; it has a very different appearance from the harpe represented in f. 18 to 26, while the difference between f. 32 and 29 is less conspicuous; the variation of the Philippine examples takes place in such a direction that some individuals approach f. 35.

Of the *males* from the Sulla Islands Mr. Rothschild says that they are not exactly identical with the Philippine *alphenor* in wing-pattern, but approach a little *P. polytes perversus*. The harpes of the Sulla *males* (f. 33) are, on the contrary, still slenderer than in Philippine *alphenor*, thus indicating that a relationship in wing-pattern is not necessarily corroborated by the development of the genital armature.

From the Southern Moluccas we had unfortunately only one individual at our disposal; the harpe of this specimen is shaped nearly as in *polytes perversus* (f. 35).

In the harpes, therefore, the *males* of *alphenor* from the three localities (Philippine Islands, Sulla Islands, and Southern Moluccas) are fairly well distinguishable, though there is no distinct line of separation.

h. *P. polytes nicanor* from Halmaheira and Batjan; f. 36.

The blade of the harpe is much higher than in *polytes alphenor*, and in this respect *nicanor* comes nearest to the Indian *polytes polytes*; the apex of the harpe is produced, nearly as in *alphenor*. F. 36 is taken from a Halmaheira individual.

6. **Papilio ambrax**; f. 37 and 38.

The outline of the valve (f. 38) of this species varies individually. The harpe is generally formed as in f. 37, but is sometimes somewhat slenderer and at the apex less hooked.

We merely give the two figures of the valve and harpe of an *ambrax* individual (from German New Guinea) in order to enable the reader to compare them with f. 18 to 36. The differences between f. 37 (*ambrax*) and 36 or 34 (*polytes*), belonging to two species, are not so conspicuous as the divergency exhibited by various harpes within the species *polytes*.

The facts of variation observed in *P. polytes* are as follows:—

(1) The valve is variable in the individual specimens, but does not exhibit in the specimens examined any obvious variation according to locality.

(2) The conspicuous individual aberration *P. polytes borealis* ♂-ab. *thibetanus* has no peculiarity in the genital armature.

(3) The individual variation in the blade of the harpe of the individuals from India is such (f. 18 and 19) that the extremes stand further apart than many individuals of *polytes polytes* do from many individuals of *polytes theseus*.

(4) The harpe of *polytes theseus* from Java and the lesser Sunda Islands is well distinguished from that of the Indian *polytes polytes*, but there is no parting line on account of the intermediate form of the harpe of *polytes theseus* from Borneo and Sumatra.

(5) Certain Timor individuals of *polytes theseus* come in the harpe (f. 30) very near *polytes perversus* from Sangir and Talaut (f. 35), and this again is very close to *polytes alcindor* from Celebes (f. 34).

(6) The harpe of *polytes alphenor* from the Philippine and Sulla Islands is in the height of the blade nearer related to *polytes theseus* from Java and the lesser Sunda Islands than to *polytes theseus* from Borneo and *alcindor* from Celebes, which subspecies are geographically the nearest to *alphenor* ; while, on the other hand, the apex of the harpe is in all the subspecies inhabiting Celebes, the Philippines, Sangir and Talaut, the Sulla Islands, and the Moluccas, somewhat curved upwards (and towards the dorsal margin of the valve), and not turned up, or rarely so, in *polytes theseus*.

(7) The subspecies most conspicuously different in the harpe is *P. polytes alphenor*, while the subspecies most conspicuously different in the shape and pattern of the wing is *P. polytes nicanor*.

7. **Papilio euchenor**; f. 51 to 64.

This insect is purely Papuan, being found in New Guinea, the Aru and Kei Islands, the D'Entrecasteaux Islands, Woodlark Island, and on New Britain and New Ireland; it has no near relative. Up to 1895 the specimens from these various localities had been treated as identical; Mr. Rothschild in his Revision found, however, that the individuals in his collection from the Bismarck Archipelago are in both sexes conspicuously different from the New Guinea specimens, and that, on the other side, the individuals from Aru are in the *female* sex, not in the *male*, also *constantly* different as far as the great material examined can be taken as furnishing a *proof* of a constancy of distinction. Lately, Mr. Rothschild observed, moreover, that the specimens from New Ireland are again in both sexes distinguishable from the individuals from New Britain ; so that there are four well recognisable forms, to which is to be added a fifth from Woodlark Island * described as a distinct species some forty years ago, but scarcely different in the ♂ in external features from the New Guinea form. The question is now, are the five forms one species, or do they belong to more species ? An answer is in this case extremely difficult to give : first, because *euchenor* stands quite isolated amongst the Indo-Australian Papilios, and thus does not allow us to compare the distinguishing characters of other forms assumed, or proved, to be specifically distinct ; secondly, because the main portion of New Britain, which geographically is nearest to New Guinea and hence may perhaps be inhabited by an *euchenor* form intermediate between the New Guinea form and the New Britain form, is entomologically an entire blank, all the specimens received from New Britain being caught in the north-east of the island. The external characters of the various forms, however, allow us to set at rest the question ; as *obsolescens* from Aru and Kei, and *godarti* from Woodlark, are in the *male* not always distinguishable from *euchenor* from New Guinea, these three forms have to be treated as subspecies of one species (the name of which is *euchenor*).

The two forms from the Bismarck Archipelago, *depilis* from New Britain and *novohibernicus* from New Ireland, have several conspicuous characters in common by which they are differentiated from *euchenor euchenor*, *euchenor obsolescens*, and *euchenor godarti*, while the differences between *depilis* and *novohibernicus* are

---

* And perhaps a sixth from the D'Entrecasteaux Islands.

(5) Certain Timor individuals of *polytes theseus* come in the harpe (f. 30) very near *polytes perversus* from Sangir and Talaut (f. 35), and this again is very close to *polytes alcindor* from Celebes (f. 34).

(6) The harpe of *polytes alphenor* from the Philippine and Sulla Islands is in the height of the blade nearer related to *polytes theseus* from Java and the lesser Sunda Islands than to *polytes theseus* from Borneo and *alcindor* from Celebes, which subspecies are geographically the nearest to *alphenor* ; while, on the other hand, the apex of the harpe is in all the subspecies inhabiting Celebes, the Philippines, Sangir and Talaut, the Sulla Islands, and the Moluccas, somewhat curved upwards (and towards the dorsal margin of the valve), and not turned up, or rarely so, in *polytes theseus*.

(7) The subspecies most conspicuously different in the harpe is *P. polytes alphenor*, while the subspecies most conspicuously different in the shape and pattern of the wing is *P. polytes nicanor*.

7. **Papilio euchenor**; f. 51 to 64.

This insect is purely Papuan, being found in New Guinea, the Aru and Kei Islands, the D'Entrecasteaux Islands, Woodlark Island, and on New Britain and New Ireland; it has no near relative. Up to 1895 the specimens from these various localities had been treated as identical; Mr. Rothschild in his Revision found, however, that the individuals in his collection from the Bismarck Archipelago are in both sexes conspicuously different from the New Guinea specimens, and that, on the other side, the individuals from Aru are in the *female* sex, not in the *male*, also *constantly* different as far as the great material examined can be taken as furnishing a *proof* of a constancy of distinction. Lately, Mr. Rothschild observed, moreover, that the specimens from New Ireland are again in both sexes distinguishable from the individuals from New Britain ; so that there are four well recognisable forms, to which is to be added a fifth from Woodlark Island * described as a distinct species some forty years ago, but scarcely different in the ♂ in external features from the New Guinea form. The question is now, are the five forms one species, or do they belong to more species ? An answer is in this case extremely difficult to give : first, because *euchenor* stands quite isolated amongst the Indo-Australian Papilios, and thus does not allow us to compare the distinguishing characters of other forms assumed, or proved, to be specifically distinct ; secondly, because the main portion of New Britain, which geographically is nearest to New Guinea and hence may perhaps be inhabited by an *euchenor* form intermediate between the New Guinea form and the New Britain form, is entomologically an entire blank, all the specimens received from New Britain being caught in the north-east of the island. The external characters of the various forms, however, allow us to set at rest the question ; as *obsolescens* from Aru and Kei, and *godarti* from Woodlark, are in the *male* not always distinguishable from *euchenor* from New Guinea, these three forms have to be treated as subspecies of one species (the name of which is *euchenor*).

The two forms from the Bismarck Archipelago, *depilis* from New Britain and *novohibernicus* from New Ireland, have several conspicuous characters in common by which they are differentiated from *euchenor euchenor*, *euchenor obsolescens*, and *euchenor godarti*, while the differences between *depilis* and *novohibernicus* are quantitatively much slighter; hence *depilis* and *novohibernicus* must (on the ground of external features) be considered as nearer related to one another than to the other *euchenor* forms. As in the present paper it is our purpose to demonstrate the variation of the genital armature within the limits of a species, and as therefore we have to avoid, as far as possible, any error as to the actual specific identity of the forms included by us in the limits of a respective species, we will, merely for the sake of being on the safe side, assume that *depilis* is a species distinct from *euchenor*. The external characters by which *novohibernicus* is distinguished from *depilis* are found in every specimen of our short series: if, therefore, the constant presence of a distinguishing character is considered sufficient to make the respective form specifically distinct (as some naturalists do), *novohibernicus* is also a distinct species. However, the distinguishing characters of *novohibernicus* amount quantitatively not to more—about the qualitative amount of these characters we know nothing—than the differences do which are observed between New Guinea individuals, differences in the extent of the yellow markings which are not thought to indicate anything else but individual variability within the same species; consequently we must assume that the differences between the individuals from New Britain and those from New Ireland being quantitatively the same are also qualitatively the same, *i.e.* do not indicate more than divergency of individuals of the same species. Hence the characters distinguishing *depilis* and *novohibernicus* must correctly be considered as not being of specific value. The various forms in question are therefore to be grouped as follows:—

---

* And perhaps a sixth from the D'Entrecasteaux Islands.

1. *P. euchenor*
   - *euchenor*; New Guinea and islands near it.
   - *godarti*; Woodlark Island.
   - *obsolescens*; Aru and Kei Islands.
2. *P. depilis*
   - *depilis*; New Britain.
   - *novohibernicus*; New Ireland.

The genital armature of the five forms is in accordance with this division.

The *valve* of *P. euchenor* (f. 51) is very large, strongly convex outwardly, with the apical margin rounded, the ventri-apical angle not being triangularly produced as in *P. aegeus* and most other species; it exhibits some individual variability in the outline, especially in the ventri-apical portion. The armature of the valve consists of a fold running along the ventral margin of the valve in a slightly oblique direction, turning near the apex round towards the dorsal edge of the valve, running from here as a thin fold backwards to the base, first in a directly basal, then in a dorso-ventral direction, and thus returning to the starting-point; from the basal dorso-ventral portion an oblique fold (f. 51, *d*) starts, traverses the (concave) valve, and widening out joins the ventral longitudinal ridge. The ventral portion is raised into a ridge, armed at both ends with a process, of which the first (*c*) is here called "basal hook," the second (*b*) "ventri-apical hook"; the basal ridge leans over ventrally, so that in a view perpendicular to the valve the dorsal surface of the ridge is visible (as in f. 51); it is highest near the basal hook (f. 52); the outline is not constant. The ventri-apical hook is directed in a basi-apical direction leaning over ventrally, with the tip protruding above the elevated edge of the valve. The vertical, ventri-dorsal, portion of the fold is less high than the ventral ridge, thinner and denticulate; it leans over apically, so that in a perpendicular view the basal surface of the ridge is visible: at the dorsal end it is produced into a slender and very sharp hook (*a*), the "dorsal hook," which is curved in an apici-ventral quantitatively much slighter; hence *depilis* and *novohibernicus* must (on the ground of external features) be considered as nearer related to one another than to the other *euchenor* forms. As in the present paper it is our purpose to demonstrate the variation of the genital armature within the limits of a species, and as therefore we have to avoid, as far as possible, any error as to the actual specific identity of the forms included by us in the limits of a respective species, we will, merely for the sake of being on the safe side, assume that *depilis* is a species distinct from *euchenor*. The external characters by which *novohibernicus* is distinguished from *depilis* are found in every specimen of our short series : if, therefore, the constant presence of a distinguishing character is considered sufficient to make the respective form specifically distinct (as some naturalists do), *novohibernicus* is also a distinct species. However, the distinguishing characters of *novohibernicus* amount quantitatively not to more—about the qualitative amount of these characters we know nothing—than the differences do which are observed between New Guinea individuals, differences in the extent of the yellow markings which are not thought to indicate anything else but individual variability within the same species ; consequently we must assume that the differences between the individuals from New Britain and those from New Ireland being quantitatively the same are also qualitatively the same, *i.e.* do not indicate more than divergency of individuals of the same species. Hence the characters distinguishing *depilis* and *novohibernicus* must correctly be considered as not being of specific value. The various forms in question are therefore to be grouped as follows :—

1. *P. euchenor*
   - *euchenor* ; New Guinea and islands near it.
   - *godarti* ; Woodlark Island.
   - *obsolescens* ; Aru and Kei Islands.
2. *P. depilis*
   - *depilis* ; New Britain.
   - *novohibernicus* ; New Ireland.

The genital armature of the five forms is in accordance with this division.

The *valve* of *P. euchenor* (f. 51) is very large, strongly convex outwardly, with the apical margin rounded, the ventri-apical angle not being triangularly produced as in *P. aegeus* and most other species ; it exhibits some individual variability in the outline, especially in the ventri-apical portion. The armature of the valve consists of a fold running along the ventral margin of the valve in a slightly oblique direction, turning near the apex round towards the dorsal edge of the valve, running from here as a thin fold backwards to the base, first in a directly basal, then in a dorso-ventral direction, and thus returning to the starting-point ; from the basal dorso-ventral portion an oblique fold (f. 51, *d*) starts, traverses the (concave) valve, and widening out joins the ventral longitudinal ridge. The ventral portion is raised into a ridge, armed at both ends with a process, of which the first (*c*) is here called "basal hook," the second (*b*) "ventri-apical hook"; the basal ridge leans over ventrally, so that in a view perpendicular to the valve the dorsal surface of the ridge is visible (as in f. 51) ; it is highest near the basal hook (f. 52) ; the outline is not constant. The ventri-apical hook is directed in a basi-apical direction leaning over ventrally, with the tip protruding above the elevated edge of the valve. The vertical, ventri-dorsal, portion of the fold is less high than the ventral ridge, thinner and denticulate ; it leans over apically, so that in a perpendicular view the basal surface of the ridge is visible : at the dorsal end it is produced into a slender and very sharp hook (*a*), the "dorsal hook," which is curved in an apici-ventral direction; just underneath the hook the ridge is highest; the number of teeth is variable.

The variation according to locality affects especially the length of the longitudinal (ventral) and the ventri-dorsal ridges, their outline and armature, and the height of the oblique fold.

a. *P. euchenor euchenor*: f. 51 to 54, 59 to 61.

The variation noticed by us in the ventral ridge of New Guinea individuals is represented in views from the dorsal side in f. 52 to 54. The usual form of the ridge is given in f. 52, taken from an example from Constantinhafen, German New Guinea (f. 51 is taken from the same individual). In f. 53, representing a specimen from the same locality, the ridge is very high in the basal third and then rather suddenly diminishes in height ; and in f. 54, taken from a specimen from Simbang, near Finschhafen, Huon Golfe, the abruptly raised basal portion is rather angulate.

Our specimens from the D'Entrecasteaux group of islands, east of New Guinea, as well as those from Waigen, west of New Guinea, come in respect to the ventral ridge within the limits of variation as illustrated by f. 52, 53, 54. All the specimens have the angle formed by the sudden break in the outline of the ridge produced into the beak-like basal hook.

The vertical (ventri-dorsal) ridge is represented separate from the ventral ridge in order to be able to give the exact outline ; f. 59, 60, 61, are taken from the same individuals as f. 52, 53, 54 respectively. As f. 59 to 61 are drawn from a basal view of the ridge, the ventri-apical hook (*b*) has a different appearance from that in f. 52 to 54.

The higher dorsal (left-hand side in figure) portion of the ridge is dentate: just at the highest point, or close to it, stands nearly always a stronger tooth, which in f. 59, however, is obsolete. The specimens from the D'Entrecasteaux Islands have nearly all the ridge toothed similarly to f. 61, a character which becomes more obvious in the individuals from Woodlark Island. The interesting aberration from Jobi Island, *P. euchenor euchenor* ab. *eutropius*, does not present any peculiarity in the valval armature.

b. *P. euchenor godarti* ; f. 58.

We have examined three specimens of this form, which is all known to exist in collections, except Montrouzier's type-specimen which is perhaps (? !) preserved in the Paris Museum. The only distinguishing character in the valve and its armature found in all three individuals concerns the oblique fold (*d*), which is higher than in either *euchenor obsolescens* or *euchenor euchenor*; the valval cavity before and behind the fold is consequently deeper. The ventral and ventri-dorsal ridges are not constantly different from those of the New Guinea individuals : the dentition of the vertical fold is, however, in all three examples rather plentiful. The more aberrant harpe of the three is represented by f. 58 and 64 ; the ventral ridge (f. 58) is distinguished by the long basal and relatively short ventri-apical hook, and by the upper edge of the ridge being feebly and widely bisinuate ; the ventri-dorsal ridge is multidentate.

c. *P. euchenor obsolescens*; f. 55, 56, 57, and 62, 63, 64.

In Aru individuals the ventral (longitudinal) ridge is somewhat shorter than in *euchenor euchenor*, and the vertical ridge accordingly longer, as will be seen by direction; just underneath the hook the ridge is highest; the number of teeth is variable.

The variation according to locality affects especially the length of the longitudinal (ventral) and the ventri-dorsal ridges, their outline and armature, and the height of the oblique fold.

a. *P. euchenor euchenor*: f. 51 to 54, 59 to 61.

The variation noticed by us in the ventral ridge of New Guinea individuals is represented in views from the dorsal side in f. 52 to 54. The usual form of the ridge is given in f. 52, taken from an example from Constantinhafen, German New Guinea (f. 51 is taken from the same individual). In f. 53, representing a specimen from the same locality, the ridge is very high in the basal third and then rather suddenly diminishes in height; and in f. 54, taken from a specimen from Simbang, near Finschhafen, Huon Golfe, the abruptly raised basal portion is rather angulate.

Our specimens from the D'Entrecasteaux group of islands, east of New Guinea, as well as those from Waigen, west of New Guinea, come in respect to the ventral ridge within the limits of variation as illustrated by f. 52, 53, 54. All the specimens have the angle formed by the sudden break in the outline of the ridge produced into the beak-like basal hook.

The vertical (ventri-dorsal) ridge is represented separate from the ventral ridge in order to be able to give the exact outline; f. 59, 60, 61, are taken from the same individuals as f. 52, 53, 54 respectively. As f. 59 to 61 are drawn from a basal view of the ridge, the ventri-apical hook (*b*) has a different appearance from that in f. 52 to 54.

The higher dorsal (left-hand side in figure) portion of the ridge is dentate: just at the highest point, or close to it, stands nearly always a stronger tooth, which in f. 59, however, is obsolete. The specimens from the D'Entrecasteaux Islands have nearly all the ridge toothed similarly to f. 61, a character which becomes more obvious in the individuals from Woodlark Island. The interesting aberration from Jobi Island, *P. euchenor euchenor* ab. *eutropius*, does not present any peculiarity in the valval armature.

b. *P. euchenor godarti*; f. 58.

We have examined three specimens of this form, which is all known to exist in collections, except Montrouzier's type-specimen which is perhaps (? !) preserved in the Paris Museum. The only distinguishing character in the valve and its armature found in all three individuals concerns the oblique fold (*d*), which is higher than in either *euchenor obsolescens* or *euchenor euchenor*; the valval cavity before and behind the fold is consequently deeper. The ventral and ventri-dorsal ridges are not constantly different from those of the New Guinea individuals: the dentition of the vertical fold is, however, in all three examples rather plentiful. The more aberrant harpe of the three is represented by f. 58 and 64; the ventral ridge (f. 58) is distinguished by the long basal and relatively short ventri-apical hook, and by the upper edge of the ridge being feebly and widely bisinuate; the ventri-dorsal ridge is multidentate.

c. *P. euchenor obsolescens*; f. 55, 56, 57, and 62, 63, 64.

In Aru individuals the ventral (longitudinal) ridge is somewhat shorter than in *euchenor euchenor*, and the vertical ridge accordingly longer, as will be seen by comparing f. 55, 56, and 62, 63, with f. 52 to 54 and 59, 60 respectively. In outline the longitudinal ridge is on the whole not different from that of New Guinea examples, but the usual form of the ridge is not that represented in f. 56, which is similar to f. 52, representing the usual form of the ridge in *euchenor euchenor*, but a form resembling f. 55. In the latter figure there is an additional tooth upon the crown of the basal dilatation of the ridge, which we have seen only in this one individual. The ventri-apical hook is in the specimens examined shorter than in *euchenor euchenor*. The vertical ridge (f. 62 and 63) shows a certain amount of variability in the dentition. The ventri-apical hook appears to be somewhat more curved towards the right-hand side than in f. 59 to 61; this is due to the hook being more erect than in *euchenor euchenor*, less leaning over ventrally and apically.

From the Kei Islands three individuals have been examined which, in external features, do not exhibit obvious differences from the Aru specimens in the Tring Museum. The harpe presents, however, in the three examples some slight distinguishing characters. The longitudinal ridge is (f. 57) still shorter than in Aru individuals, the ventri-apical hook stands still more erect to the plane of the valve and the upper edge of the ventral ridge (as will be seen both from f. 57 and f. 64), and the vertical ridge (f. 64) is provided with many strong teeth.

8. **Papilio depilis**; f. 65 to 71.

The *valve* is ventrally a little more rounded than in *P. euchenor*, but this character is not constant. The armature of the valve (f. 65) is, however, obviously different. A comparison of f. 51 and 65 will show that the valves with the armature are in both species closely related; there are the same folds, ridges, and hooks in *depilis* which we have found in *euchenor*, but the organs have differently developed. The ventral (longitudinal) and apical (vertical) ridges of *euchenor* stand in *depilis* both so oblique that the angle formed by them in *euchenor* has almost disappeared. The ventri-apical hook does not lean over to the ventri-apical side of the valve, but to the dorsal side, so that the point of the hook will in *depilis* meet in copulation quite a different spot in the vaginal region of the *female* than in *euchenor*. The dentate vertical ridge is much shorter (f. 70, 71), sinuate in or near the middle, with the two higher parts at the side of the sinus dentate. The oblique fold (*d*) joins the ventral ridge near the apex (f. 66 to 69), not in the middle as in f. 52 to 58, and is basally not rounded but strongly compressed.

a. *P. depilis depilis*; f. 65 to 67, and 70.

The ventral ridge is throughout its length very high; its outline is variable. In f. 66 the upper edge of the ridge is undulate; the basal angle (*e*) is without the beak-like hook found in every specimen of *euchenor*. In a second individual (f. 67) the basal hook is indicated by a very minute tooth; in the middle the ridge is triangularly dilated. In a third specimen (not figured) the ridge is again without the basal hook, and is in the middle also higher than at the basal angle, but not so triangularly dilated as in the second example.

The ventri-dorsal dentate ridge (f. 70) leans strongly over to the apical side of the valve, and hence appears less high than in *euchenor*, but there are specimens of *euchenor* which in this respect are scarcely different from *depilis*. Besides the dorsal hook (*a*) there are three longer subdorsal and two smaller subventral teeth separated by a sinus; in a second specimen these teeth are all obsolete, while in a third only two are present.

comparing f. 55, 56, and 62, 63, with f. 52 to 54 and 59, 60 respectively. In outline the longitudinal ridge is on the whole not different from that of New Guinea examples, but the usual form of the ridge is not that represented in f. 56, which is similar to f. 52, representing the usual form of the ridge in *euchenor euchenor*, but a form resembling f. 55. In the latter figure there is an additional tooth upon the crown of the basal dilatation of the ridge, which we have seen only in this one individual. The ventri-apical hook is in the specimens examined shorter than in *euchenor euchenor*. The vertical ridge (f. 62 and 63) shows a certain amount of variability in the dentition. The ventri-apical hook appears to be somewhat more curved towards the right-hand side than in f. 59 to 61; this is due to the hook being more erect than in *euchenor euchenor*, less leaning over ventrally and apically.

From the Kei Islands three individuals have been examined which, in external features, do not exhibit obvious differences from the Aru specimens in the Tring Museum. The harpe presents, however, in the three examples some slight distinguishing characters. The longitudinal ridge is (f. 57) still shorter than in Aru individuals, the ventri-apical hook stands still more erect to the plane of the valve and the upper edge of the ventral ridge (as will be seen both from f. 57 and f. 64), and the vertical ridge (f. 64) is provided with many strong teeth.

8. **Papilio depilis**; f. 65 to 71.

The *valve* is ventrally a little more rounded than in *P. euchenor*, but this character is not constant. The armature of the valve (f. 65) is, however, obviously different. A comparison of f. 51 and 65 will show that the valves with the armature are in both species closely related; there are the same folds, ridges, and hooks in *depilis* which we have found in *euchenor*, but the organs have differently developed. The ventral (longitudinal) and apical (vertical) ridges of *euchenor* stand in *depilis* both so oblique that the angle formed by them in *euchenor* has almost disappeared. The ventri-apical hook does not lean over to the ventri-apical side of the valve, but to the dorsal side, so that the point of the hook will in *depilis* meet in copulation quite a different spot in the vaginal region of the *female* than in *euchenor*. The dentate vertical ridge is much shorter (f. 70, 71), sinuate in or near the middle, with the two higher parts at the side of the sinus dentate. The oblique fold (*d*) joins the ventral ridge near the apex (f. 66 to 69), not in the middle as in f. 52 to 58, and is basally not rounded but strongly compressed.

a. *P. depilis depilis*; f. 65 to 67, and 70.

The ventral ridge is throughout its length very high; its outline is variable. In f. 66 the upper edge of the ridge is undulate; the basal angle (*e*) is without the beak-like hook found in every specimen of *euchenor*. In a second individual (f. 67) the basal hook is indicated by a very minute tooth; in the middle the ridge is triangularly dilated. In a third specimen (not figured) the ridge is again without the basal hook, and is in the middle also higher than at the basal angle, but not so triangularly dilated as in the second example.

The ventri-dorsal dentate ridge (f. 70) leans strongly over to the apical side of the valve, and hence appears less high than in *euchenor*, but there are specimens of *euchenor* which in this respect are scarcely different from *depilis*. Besides the dorsal hook (*a*) there are three longer subdorsal and two smaller subventral teeth separated by a sinus; in a second specimen these teeth are all obsolete, while in a third only two are present.

b. *P. depilis novohibernicus*; f. 68, 69, and 71.

The harpe is very slightly different from that of *depilis depilis*; the portion of the ventral ridge which is produced into the ventri-apical hook forms a slight angle with the basal portion of the ridge, being a little more curved dorsally than in *depilis depilis*; the vertical dentate ridge is shorter than in that subspecies.

In three out of four examples the ventral ridge is highest beyond the middle, as in f. 68 and 69 ; while in the fourth specimen the dilatation takes place before the middle in a somewhat similar way as in f. 53. The basal hook (*c*) is in f. 68 scarcely indicated; in f. 68 it is as strong as in many *euchenor*. The dorsal ridge is generally shaped as in f. 71, but the teeth are sometimes much feebler than in the figure.

The facts of variation illustrated by f. 51 to 71 are as follows :—

(1) In the two closely allied species *P. euchenor* and *P. depilis* the armature of the valve is built up after exactly the same plan, but in the detail of structure there are conspicuous differences.

(2) The subspecies of *euchenor* from New Guinea and that from Woodlark present in the specimens examined no constant difference except in the oblique fold (*d*) ; the subspecies from Aru is so slightly different that the distinguishing character is scarcely noticeable if one does not compare several specimens; the Kei Island individuals are more obviously different than the Aru specimens (and represent probably another local form). The two subspecies of *depilis* are, according to the seven specimens examined, slightly different in the *male* genital armature.

(3) The individual variation within each subspecies is such that the differences between the harpes of several individuals from the same place (and hence most certainly belonging to the same species) are more obvious than those of the subspecies *inter se*.

(4) The only specimen known of the aberration *P. euchenor euchenor* ab. *eutropius*, which is abnormal in the pattern of the forewing, does not present any peculiarity in the genital armature.

9. **Papilio cloanthus** ; f. 149 to 155.

The range of this insect is rather widely interrupted, the species being found all over North India, Upper Burma, and Central and Western China, and again in the mountainous regions of N.E. Sumatra; from the mountains of Malacca, Tenasserim, and Siam *P. cloanthus* is not known. The external features of the specimens from the various localities are such that we can group the individuals according to locality in three forms: an Indian, a Chinese, and a Sumatran form. The first two are not always distinguishable in pattern, and hence are certainly not specifically distinct from one another. The Sumatran specimens, at least all individuals of our long series (forty odd examples), are constantly different in the colour and extent of the markings; the divergency from Indian specimens is, however, not very conspicuous, which will be admitted if we call to mind that de Nicéville * especially says that the Sumatran insect is " identical " with the Indian one. As the minuteness of the distinguishing characters of the insect is, according to what has been said in the introductory notes, *a priori* no objection to the constantly found characters being of specific value, there must be other reasons brought forward which

---

* *Journ. As. Soc. Beng.* p. 526, n. 607 (1896).

b. *P. depilis novohibernicus*; f. 68, 69, and 71.

The harpe is very slightly different from that of *depilis depilis*; the portion of the ventral ridge which is produced into the ventri-apical hook forms a slight angle with the basal portion of the ridge, being a little more curved dorsally than in *depilis depilis*; the vertical dentate ridge is shorter than in that subspecies.

In three out of four examples the ventral ridge is highest beyond the middle, as in f. 68 and 69 ; while in the fourth specimen the dilatation takes place before the middle in a somewhat similar way as in f. 53. The basal hook (*c*) is in f. 68 scarcely indicated; in f. 68 it is as strong as in many *euchenor*. The dorsal ridge is generally shaped as in f. 71, but the teeth are sometimes much feebler than in the figure.

The facts of variation illustrated by f. 51 to 71 are as follows :—

(1) In the two closely allied species *P. euchenor* and *P. depilis* the armature of the valve is built up after exactly the same plan, but in the detail of structure there are conspicuous differences.

(2) The subspecies of *euchenor* from New Guinea and that from Woodlark present in the specimens examined no constant difference except in the oblique fold (*d*) ; the subspecies from Aru is so slightly different that the distinguishing character is scarcely noticeable if one does not compare several specimens; the Kei Island individuals are more obviously different than the Aru specimens (and represent probably another local form). The two subspecies of *depilis* are, according to the seven specimens examined, slightly different in the *male* genital armature.

(3) The individual variation within each subspecies is such that the differences between the harpes of several individuals from the same place (and hence most certainly belonging to the same species) are more obvious than those of the subspecies *inter se*.

(4) The only specimen known of the aberration *P. euchenor euchenor* ab. *eutropius*, which is abnormal in the pattern of the forewing, does not present any peculiarity in the genital armature.

9. **Papilio cloanthus** ; f. 149 to 155.

The range of this insect is rather widely interrupted, the species being found all over North India, Upper Burma, and Central and Western China, and again in the mountainous regions of N.E. Sumatra; from the mountains of Malacca, Tenasserim, and Siam *P. cloanthus* is not known. The external features of the specimens from the various localities are such that we can group the individuals according to locality in three forms: an Indian, a Chinese, and a Sumatran form. The first two are not always distinguishable in pattern, and hence are certainly not specifically distinct from one another. The Sumatran specimens, at least all individuals of our long series (forty odd examples), are constantly different in the colour and extent of the markings; the divergency from Indian specimens is, however, not very conspicuous, which will be admitted if we call to mind that de Nicéville * especially says that the Sumatran insect is " identical " with the Indian one. As the minuteness of the distinguishing characters of the insect is, according to what has been said in the introductory notes, *a priori* no objection to the constantly found characters being of specific value, there must be other reasons brought forward which

* *Journ. As. Soc. Beng.* p. 526. n. 607 (1896).

force us to treat the Sumatran form not as a separate species. North Indian *cloanthus* occur in several broods; the individuals of the spring and those of the summer broods are in the extent of the markings rather obviously different, and this proves that the species is in pattern easily modified by the transmuting factors; the extreme individuals of the spring brood differ in the extent of the markings more from the extreme examples of the summer brood than certain Indian individuals do from certain Sumatran ones. Further, the differences of certain Chinese specimens from Indian individuals are quantitatively greater than those between Indian and Sumatran examples. Hence it is correct to accept Mr. Rothschild's opinion * and to treat the three insects in question as three subspecies of *P. cloanthus*.

The valve (f. 149) of *P. cloanthus* is, as in all the allied species, rather small; at the apex it is deeply sinuate. The sinus divides the apical third of the valve in a smaller dorsal lobe (*b*) and a larger ventral lobe (*a*). The ventral edge of the valve is angulate (*f*), and from this angle to the tip of the ventral lobe densely beset with irregular rows of thin and sharp teeth. The internal sheath of the valve is raised into a distinct fold (*e*), which begins ventrally at the base—in f. 149 and 150 the right-hand side is the ventral side of the valve—runs for a short distance along the ventral margin of the valve, turns in a rather even curve round towards the dorsal side, forms a subdorsal tooth (*c*), and then traverses longitudinally the dorsal lobe, being here raised into a short dentate ridge (*d*), the "dorsal ridge" which stands almost perpendicular upon the plane of the lobe leaning very feebly over ventrally. In f. 149 and 150 the subdorsal tooth (*c*) is visible almost in its entire length, because it is bent over apically, while the dorsal ridge appears much less high than it really is.

The variation of the species according to locality relates especially to the form of the valve, the length of the subdorsal tooth, and the form of the dorsal ridge.

a. *P. cloanthus cloanthus* from Kulu to the Shan States, at higher elevations: f. 149, 151, 152.

The sinus of the valve is $\frac{3}{4}$ mm. deep. The ventri-dorsal fold (*e*) is slightly curved. The subdorsal tooth (*c*) is high, simple, and when seen from the dorsal side, as in f. 151 and 152, reaches so far that its tip appears to be above the dorsal ridge. The length of the tooth is variable: the lower extreme met with by us is represented by f. 152 (Shan States); in a second individual from the Shan States the tooth is nearly as long as in f. 151, which is taken from a Sikkim specimen and represents the usual form of the tooth. As both the Chinese and Sumatran subspecies have the tooth generally considerably shorter, the mountainous regions of Siam, Tenasserim, and Malacca on the one side, and of Upper Tonkin on the other, will most probably yield (if inhabited by *cloanthus*) individuals more often, or even constantly, intermediate between the three subspecies in respect to the length of the tooth.

The dorsal ridge (f. 151, 152) of *cloanthus cloanthus* is a little longer than high, and is in all our specimens rather strongly denticulate.

The individuals of the spring brood are not different in the valve and harpe from the individuals of the later broods.

b. *P. cloanthus clymenus* from Western and Central China; f. 153.

In the outline of the valve all the individuals examined agree with specimens force us to treat the Sumatran form not as a separate species. North Indian *cloanthus* occur in several broods; the individuals of the spring and those of the summer broods are in the extent of the markings rather obviously different, and this proves that the species is in pattern easily modified by the transmuting factors; the extreme individuals of the spring brood differ in the extent of the markings more from the extreme examples of the summer brood than certain Indian individuals do from certain Sumatran ones. Further, the differences of certain Chinese specimens from Indian individuals are quantitatively greater than those between Indian and Sumatran examples. Hence it is correct to accept Mr. Rothschild's opinion * and to treat the three insects in question as three subspecies of *P. cloanthus*.

---

* Nov. Zool. p. 445 (1895).

The valve (f. 149) of *P. cloanthus* is, as in all the allied species, rather small; at the apex it is deeply sinuate. The sinus divides the apical third of the valve in a smaller dorsal lobe (*b*) and a larger ventral lobe (*a*). The ventral edge of the valve is angulate (*f*), and from this angle to the tip of the ventral lobe densely beset with irregular rows of thin and sharp teeth. The internal sheath of the valve is raised into a distinct fold (*e*), which begins ventrally at the base—in f. 149 and 150 the right-hand side is the ventral side of the valve—runs for a short distance along the ventral margin of the valve, turns in a rather even curve round towards the dorsal side, forms a subdorsal tooth (*c*), and then traverses longitudinally the dorsal lobe, being here raised into a short dentate ridge (*d*), the "dorsal ridge" which stands almost perpendicular upon the plane of the lobe leaning very feebly over ventrally. In f. 149 and 150 the subdorsal tooth (*c*) is visible almost in its entire length, because it is bent over apically, while the dorsal ridge appears much less high than it really is.

The variation of the species according to locality relates especially to the form of the valve, the length of the subdorsal tooth, and the form of the dorsal ridge.

a. *P. cloanthus cloanthus* from Kulu to the Shan States, at higher elevations: f. 149, 151, 152.

The sinus of the valve is ¾ mm. deep. The ventri-dorsal fold (*e*) is slightly curved. The subdorsal tooth (*c*) is high, simple, and when seen from the dorsal side, as in f. 151 and 152, reaches so far that its tip appears to be above the dorsal ridge. The length of the tooth is variable: the lower extreme met with by us is represented by f. 152 (Shan States); in a second individual from the Shan States the tooth is nearly as long as in f. 151, which is taken from a Sikkim specimen and represents the usual form of the tooth. As both the Chinese and Sumatran subspecies have the tooth generally considerably shorter, the mountainous regions of Siam, Tenasserim, and Malacca on the one side, and of Upper Tonkin on the other, will most probably yield (if inhabited by *cloanthus*) individuals more often, or even constantly, intermediate between the three subspecies in respect to the length of the tooth.

The dorsal ridge (f. 151, 152) of *cloanthus cloanthus* is a little longer than high, and is in all our specimens rather strongly denticulate.

The individuals of the spring brood are not different in the valve and harpe from the individuals of the later broods.

b. *P. cloanthus clymenus* from Western and Central China; f. 153.

In the outline of the valve all the individuals examined agree with specimens of *cloanthus cloanthus*, and so they do in the form of the ventri-dorsal fold. The subdorsal tooth is in every specimen shorter than that of f. 151 (normal length of tooth of *cloanthus cloanthus*), but there occur individuals which have the tooth nearly as long as it is in f. 152. A specimen of *cloanthus clymenus* with the tooth of a length which is normal for *clymenus* is represented by f. 153. We have examined some individuals which externally are not different from Sikkim specimens, and observed the highly interesting fact that in these individuals the tooth is as short as in f. 153, while in some other examples which differ in the extent of the black colour on the wings considerably from *cloanthus cloanthus* the tooth approaches in length that of f. 152. This is a remarkable illustration of what we have said in the introduction, namely that specimens can be similar or identical in one set of characters, while in another, independent, set they are dissimilar; the Chinese individuals of *cloanthus* which in pattern are like Indian *cloanthus cloanthus* are nevertheless individuals of *cloanthus clymenus*, distinguished from *cloanthus cloanthus* by a character of the genital armature not found, to our knowledge, in any individuals from India. We shall have to refer again to this fact later on.

---

* Nov. Zool. p. 445 (1895).

The dorsal ridge of the Chinese *cloanthus* is similar to that of the Indian specimens; we have not found any difference that can be pronounced constant; in many individuals the ridge is a very little longer, and the teeth are often more numerous and smaller.

c. *P. cloanthus sumatranus* from the mountainous districts of N.E. Sumatra: f. 150, 154, 155.

The sinus of the valve is much smaller than in the two preceding subspecies: the dorsal edge of the dorsal lobe is more rounded, and the ventral lobe is considerably blunter. The dentition of the ventral edge of the valve is, especially near the blunt angle (*f*), extended upon the outside of the valve to such a degree that five or six small, but strongly chitinised, teeth stand irregularly one above the other.

The ventri-dorsal fold (*c*) is straighter and more raised than in *cloanthus cloanthus* and *cloanthus clymenus*, its edge is less rounded off and, especially near the subdorsal tooth, slightly notched or faintly denticulate.

The subdorsal tooth is as short as in *cloanthus clymenus*, but at the base broader, in consequence of the fold, of which it is a process, being higher; mostly it bears two or three faint teeth at the ventral edge.

The dorsal ridge is obviously shorter than in the rest of the species, but is of the same height; the free edge is less dentate, often simply sinuate. F. 154 and 155 illustrate the degree of variation in the dorsal ridge and the subdorsal tooth noticed by us.

The principal facts of variation as illustrated by f. 149 to 155 are as follows:—

(1) The three subspecies of *P. cloanthus* agree in the valve and its armature, but exhibit some differences in the detail of structure.

(2) The Indian and the Chinese forms differ constantly in the length of the subdorsal tooth, though the extremes come very close.

(3) The Sumatran form is aberrant in the form of the valve, the ventri-dorsal ridge, the subdorsal tooth, and the dorsal ridge.

(4) In the length of the subdorsal tooth the Sumatran and Chinese forms agree with one another, while they disagree with the Indian subspecies which inhabits interjacent countries.

of *cloanthus cloanthus*, and so they do in the form of the ventri-dorsal fold. The subdorsal tooth is in every specimen shorter than that of f. 151 (normal length of tooth of *cloanthus cloanthus*), but there occur individuals which have the tooth nearly as long as it is in f. 152. A specimen of *cloanthus clymenus* with the tooth of a length which is normal for *clymenus* is represented by f. 153. We have examined some individuals which externally are not different from Sikkim specimens, and observed the highly interesting fact that in these individuals the tooth is as short as in f. 153, while in some other examples which differ in the extent of the black colour on the wings considerably from *cloanthus cloanthus* the tooth approaches in length that of f. 152. This is a remarkable illustration of what we have said in the introduction, namely that specimens can be similar or identical in one set of characters, while in another, independent, set they are dissimilar; the Chinese individuals of *cloanthus* which in pattern are like Indian *cloanthus cloanthus* are nevertheless individuals of *cloanthus clymenus*, distinguished from *cloanthus cloanthus* by a character of the genital armature not found, to our knowledge, in any individuals from India. We shall have to refer again to this fact later on.

The dorsal ridge of the Chinese *cloanthus* is similar to that of the Indian specimens; we have not found any difference that can be pronounced constant; in many individuals the ridge is a very little longer, and the teeth are often more numerous and smaller.

c. *P. cloanthus sumatranus* from the mountainous districts of N.E. Sumatra: f. 150, 154, 155.

The sinus of the valve is much smaller than in the two preceding subspecies: the dorsal edge of the dorsal lobe is more rounded, and the ventral lobe is considerably blunter. The dentition of the ventral edge of the valve is, especially near the blunt angle (*f*), extended upon the outside of the valve to such a degree that five or six small, but strongly chitinised, teeth stand irregularly one above the other.

The ventri-dorsal fold (*c*) is straighter and more raised than in *cloanthus cloanthus* and *cloanthus clymenus*, its edge is less rounded off and, especially near the subdorsal tooth, slightly notched or faintly denticulate.

The subdorsal tooth is as short as in *cloanthus clymenus*, but at the base broader, in consequence of the fold, of which it is a process, being higher; mostly it bears two or three faint teeth at the ventral edge.

The dorsal ridge is obviously shorter than in the rest of the species, but is of the same height; the free edge is less dentate, often simply sinuate. F. 154 and 155 illustrate the degree of variation in the dorsal ridge and the subdorsal tooth noticed by us.

The principal facts of variation as illustrated by f. 149 to 155 are as follows:—

(1) The three subspecies of *P. cloanthus* agree in the valve and its armature, but exhibit some differences in the detail of structure.

(2) The Indian and the Chinese forms differ constantly in the length of the subdorsal tooth, though the extremes come very close.

(3) The Sumatran form is aberrant in the form of the valve, the ventri-dorsal ridge, the subdorsal tooth, and the dorsal ridge.

(4) In the length of the subdorsal tooth the Sumatran and Chinese forms agree with one another, while they disagree with the Indian subspecies which inhabits interjacent countries.

(5) The individual variation of the genital armature in the Chinese subspecies is entirely independent of external characters.

(6) The seasonal dimorphism in external characters obviously marked in the Indian *P. cloanthus cloanthus* does not affect the genital armature in any way, as far as we could ascertain.

10. **Papilio sarpedon**; f. 96 to 148.

Though some people have treated *P. sarpedon* and *P. cloanthus* as belonging to two different genera, the insects are, nevertheless, very closely allied to one another, more closely than to any other species. This does not only follow from a careful comparison of the wing-pattern of the two Papilios, but also from the structure.

The range of *P. sarpedon* comprises the whole of the Indo-Australian Region, including Japan (except the north of it). The number of subspecies into which the insect has developed is very great. As it is one of the commonest species we could examine a large number of specimens, and to this it is due that we here came across an individual which stands in the genital armature far outside the usual limits of variation of the subspecies to which it belongs.

If we select some of the extreme forms here treated as subspecies of one species, for example the Indian, Celebensian, and the Solomon Island forms, their external differences are so very conspicuous that one might easily be misled to consider these forms specifically distinct. A comparison of the representatives from all the various localities, however, convinces us that the differences in colour, pattern, shape, and size between every two nearest allied forms are very slight, and do in some forms not even apply to every specimen; and we observe further that, where the differences are constantly met with, the characters amount quantitatively not to more than the differences between the seasonal forms of Japanese *sarpedon*, or than the differences found between certain Indian examples. Hence we think it to be quite correct to accept Mr. Rothschild's statement that all the forms dealt with in the following lines are subspecies of one species.

As we now are acquainted with the more simple armature of the valve of *P. cloanthus*, that of *P. sarpedon* will be more easily understood. A comparison of f. 96 and 149 will at a glance show the great similarity in the apparatus of the two species. The valve, though differing in outline from that of *P. cloanthus*, has the same apical sinus, and the armature has nearly the same position.

The ventral lobe of the valve (f. 96, *a*) is longer, mostly broader, than the dorsal one (*b*): its ventral edge is denticulate, as in *cloanthus*, but there is only one row of teeth, and the toothed portion extends farther down towards the base. There is a good deal of variation in the shape of the lobes and the depth of the sinus, both in respect to individuals and to geographical races.

The fold (*e*) formed by the inner sheath of the valve begins ventrally at the base of the valve, as in *cloanthus*, runs in an oblique direction to somewhat beyond half-way to the apex, turns round here towards the dorsal side, forms, when having arrived at a level with the ventral margin of the dorsal lobe, a subdorsal tooth (*c*), and then is continued in a longitudinal direction to form a dorsal ridge (*d*). The homology of the organs is obvious. The fold *e* is homologous to the fold *e* in *cloanthus*, but is here less raised, takes a somewhat different course, and is at the point where it curves round towards the dorsal side often feebly toothed. The

(5) The individual variation of the genital armature in the Chinese subspecies is entirely independent of external characters.

(6) The seasonal dimorphism in external characters obviously marked in the Indian *P. cloanthus cloanthus* does not affect the genital armature in any way, as far as we could ascertain.

10. **Papilio sarpedon**; f. 96 to 148.

Though some people have treated *P. sarpedon* and *P. cloanthus* as belonging to two different genera, the insects are, nevertheless, very closely allied to one another, more closely than to any other species. This does not only follow from a careful comparison of the wing-pattern of the two Papilios, but also from the structure.

The range of *P. sarpedon* comprises the whole of the Indo-Australian Region, including Japan (except the north of it). The nnmber of subspecies into which the insect has developed is very great. As it is one of the commonest species we could examine a large number of specimens, and to this it is due that we here came across an individual which stands in the genital armature far outside the usual limits of variation of the subspecies to which it belongs.

If we select some of the extreme forms here treated as subspecies of one species, for example the Indian, Celebensian, and the Solomon Island forms, their external differences are so very conspicuous that one might easily be misled to consider these forms specifically distinct. A comparison of the representatives from all the various localities, however, convinces us that the differences in colour, pattern, shape, and size between every two nearest allied forms are very slight, and do in some forms not even apply to every specimen ; and we observe further that, where the differences are constantly met with, the characters amount quantitatively not to more than the differences between the seasonal forms of Japanese *sarpedon*, or than the differences found between certain Indian examples. Hence we think it to be quite correct to accept Mr. Rothschild's statement that all the forms dealt with in the following lines are subspecies of one species.

As we now are acquainted with the more simple armature of the valve of *P. cloanthus*, that of *P. sarpedon* will be more easily understood. A comparison of f. 96 and 149 will at a glance show the great similarity in the apparatus of the two species. The valve, though differing in outline from that of *P. cloanthus*, has the same apical sinus, and the armature has nearly the same position.

The ventral lobe of the valve (f. 96, *a*) is longer, mostly broader, than the dorsal one (*b*) : its ventral edge is denticulate, as in *cloanthus*, but there is only one row of teeth, and the toothed portion extends farther down towards the base. There is a good deal of variation in the shape of the lobes and the depth of the sinus, both in respect to individuals and to geographical races.

The fold (*e*) formed by the inner sheath of the valve begins ventrally at the base of the valve, as in *cloanthus*, runs in an oblique direction to somewhat beyond half-way to the apex, turns round here towards the dorsal side, forms, when having arrived at a level with the ventral margin of the dorsal lobe, a subdorsal tooth (*c*), and then is continued in a longitudinal direction to form a dorsal ridge (*d*). The homology of the organs is obvious. The fold *e* is homologous to the fold *e* in *cloanthus*, but is here less raised, takes a somewhat different course, and is at the point where it curves round towards the dorsal side often feebly toothed. The subdorsal tooth corresponds to that of *cloanthus*, but is here much less chitinised, usually broadened at the tip, and is in fact a dilatation of the fold *e* partly rolled in so as to form a half-cylinder; though this tooth is variable, we shall not refer to it under each subspecies. The dorsal ridge corresponds to the dorsal ridge of *cloanthus*, but is here of a more complicated structure. In a view from the dorsal side (f. 97) it will be seen that the dorsal ridge of f. 96 consists of a dentate high basal portion and a free rod-like apical process (*g*), the *dorso-apical process*, which is curved upwards—that means towards median plane of the abdomen—is denticulate at the tip, and protrudes beyond the tip of the dorsal lobe. At the ventral side of the dorsal ridge a longitudinal fold (f. 96, *i*, and 98, *i*) will be noticed which is continued to the apex of the dorsal lobe; that vertical portion of the fold (f. 98, *h*) which runs up to the upper edge of the ridge is of high importance, as it develops in most subspecies to a peculiar organ.

a. *P. sarpedon sarpedon*; f. 96 to 114.

This form occurs all over India (except S. India and Ceylon) to Java, the Philippine Islands, and Japan; in China it is replaced by another subspecies. There are some external characters by which the individuals from Java, Borneo, and the Philippines can be distinguished from the individuals from N.W. India and N. India, but these characters are very slight; besides, the Malayan individuals lead over to the more different forms from the lesser Sunda Islands, and hence remain best included in *sarpedon sarpedon*. The genital armature is entirely in accordance with this statement.

We have examined specimens from N.W. India, Sikkim, Assam, Burma, Shan States, Tenasserim, Cochin China, Sumatra, Nias, Java, Natuna Islands, Borneo, Palawan, Mindoro, Luzon, the Riu Kiu Islands (= Loo Choo Islands), and Japan. The specimens from all these localities agree so well with one another, apart from individual peculiarities, that we did not succeed in finding in the genital armature any character by which the specimens from one or the other place could be recognised.

The outline of the valve normally met with in *sarpedon sarpedon* is represented by f. 96, which is taken from a Kumaon individual. The sinus is about $\frac{1}{2}$ mm. deep; the dorsal lobe is rounded at the apex; the ventral one is also rounded, its ventral edge feebly incurved. The dorsal ridge is in the dentition very variable; the important feature is that normally the lateral fold *h* of f. 98 is very slight and incomplete, as in f. 99, or even absent.

The variability in the form of the valve is illustrated by f. 96, 97, 113, and 114. In f. 97, taken from an example from the Shan States, the sinus is narrow, and the apex of the ventral lobe also very narrow. F. 113 and 114 represent two other Shan States specimens: one has the ventral lobe much produced, and the sinus accordingly deep; in the other the same lobe is very short and broadly rounded. In the individuals from the Malayan region the ventral lobe is often, but by no means regularly, more produced and slenderer than in the average Indian specimen; and this is not surprising, as in the various subspecies from the lesser Sunda Islands the lobes are constantly long and slender.

The variation of the dentition of the dorsal ridge is very great, as will be seen from f. 98 to 100 and 101 to 110. Sikkim specimens are represented by f. 99, 100, and 108; individuals from the Shan States by f. 105 and 106; a Malacca specimen by f. 107; two Bornean examples (from Mount Mulu) by f. 109 and 110.

subdorsal tooth corresponds to that of *cloanthus*, but is here much less chitinised, usually broadened at the tip, and is in fact a dilatation of the fold *e* partly rolled in so as to form a half-cylinder; though this tooth is variable, we shall not refer to it under each subspecies. The dorsal ridge corresponds to the dorsal ridge of *cloanthus*, but is here of a more complicated structure. In a view from the dorsal side (f. 97) it will be seen that the dorsal ridge of f. 96 consists of a dentate high basal portion and a free rod-like apical process (*g*), the *dorso-apical process*, which is curved upwards—that means towards median plane of the abdomen—is denticulate at the tip, and protrudes beyond the tip of the dorsal lobe. At the ventral side of the dorsal ridge a longitudinal fold (f. 96, *i*, and 98, *i*) will be noticed which is continued to the apex of the dorsal lobe; that vertical portion of the fold (f. 98, *h*) which runs up to the upper edge of the ridge is of high importance, as it develops in most subspecies to a peculiar organ.

a. *P. sarpedon sarpedon*; f. 96 to 114.

This form occurs all over India (except S. India and Ceylon) to Java, the Philippine Islands, and Japan; in China it is replaced by another subspecies. There are some external characters by which the individuals from Java, Borneo, and the Philippines can be distinguished from the individuals from N.W. India and N. India, but these characters are very slight; besides, the Malayan individuals lead over to the more different forms from the lesser Sunda Islands, and hence remain best included in *sarpedon sarpedon*. The genital armature is entirely in accordance with this statement.

We have examined specimens from N.W. India, Sikkim, Assam, Burma, Shan States, Tenasserim, Cochin China, Sumatra, Nias, Java, Natuna Islands, Borneo, Palawan, Mindoro, Luzon, the Riu Kiu Islands (= Loo Choo Islands), and Japan. The specimens from all these localities agree so well with one another, apart from individual peculiarities, that we did not succeed in finding in the genital armature any character by which the specimens from one or the other place could be recognised.

The outline of the valve normally met with in *sarpedon sarpedon* is represented by f. 96, which is taken from a Kumaon individual. The sinus is about ½ mm. deep; the dorsal lobe is rounded at the apex; the ventral one is also rounded, its ventral edge feebly incurved. The dorsal ridge is in the dentition very variable; the important feature is that normally the lateral fold *h* of f. 98 is very slight and incomplete, as in f. 99, or even absent.

The variability in the form of the valve is illustrated by f. 96, 97, 113, and 114. In f. 97, taken from an example from the Shan States, the sinus is narrow, and the apex of the ventral lobe also very narrow. F. 113 and 114 represent two other Shan States specimens: one has the ventral lobe much produced, and the sinus accordingly deep; in the other the same lobe is very short and broadly rounded. In the individuals from the Malayan region the ventral lobe is often, but by no means regularly, more produced and slenderer than in the average Indian specimen; and this is not surprising, as in the various subspecies from the lesser Sunda Islands the lobes are constantly long and slender.

The variation of the dentition of the dorsal ridge is very great, as will be seen from f. 98 to 100 and 101 to 110. Sikkim specimens are represented by f. 99, 100, and 108; individuals from the Shan States by f. 105 and 106; a Malacca specimen by f. 107; two Bornean examples (from Mount Mulu) by f. 109 and 110.

Every individual specimen examined exhibited some peculiarity in the number, size, and form of the teeth of the dorsal ridge.

The lateral (ventral) fold (*h*) of the dorsal ridge (f. 98) is in f. 107 (Taiping, Malay Peninsula) absent, in f. 99 (Sikkim) very short, in f. 106 (Shan States) complete but very slightly raised, and is more distinct in f. 98 (Kumaon). In f. 100 (Sikkim) the fold runs up to a small tooth, which has a somewhat transverse position to the longitudinal ridge; in f. 108 the fold is raised to a low but obvious dentate ridge, which we shall call "*transverse ridge*."

In a Mindoro specimen caught by Mr. A. Everett in December 1894 the additional transverse ridge is raised above the level of the dorsal ridge, and forms a conspicuous, broad, tooth-like prominence; in f. 111 the dorsal ridge with the transverse prominence is represented in a view vertical upon the plane of the valve; and in f. 112 we give a view of the same organ from the apical side (with the eye a little above the valve).

Still more aberrant is a specimen from the Shan States caught by Mr. Roberts in the same district where the individual was obtained from which f. 106 is taken. The increase in the size of the transverse ridge, as illustrated by f. 107, 99, 106, 98, 100, 108, 111, and 112, reaches in f. 101 to 103 the maximum. The transverse ridge *h* is higher, strongly dentate, and more extended than the dentate portion of the dorsal ridge *d*: in f. 101 the organ is seen from above, in f. 102 from the ventral side, and in f. 103 from the apical side (compare f. 111 and 112).

We have examined more than a hundred specimens of *P. sarpedon sarpedon*, and found only one that has the additional transverse ridge so extraordinarily developed; the significance of this variation is obvious if we compare the special structure of the dorsal ridge of *P. sarpedon anthedon*, *milon*, *choredon*, *teredon*, etc. We shall have to refer to this particular case again.

b. *P. sarpedon semifasciatus* from China.

The Chinese subspecies of *sarpedon* is in the markings not always distinguishable from *sarpedon sarpedon*, but the greater number of the individuals from Central and Western China have a very remarkable character in the band of the hindwing being more or less obliterated. Such specimens with almost entirely black hindwings are, in respect to pattern, quantitatively more different from *sarpedon sarpedon* than the individuals of any other subspecies are. Though we dissected a long series of Chinese individuals, we did not perceive any character in the genital armature by which they could be differentiated from *sarpedon sarpedon*; and this concerns the examples which are most aberrant in pattern, as well as specimens with the ordinary *sarpedon sarpedon* pattern. The fact is of high interest, as it distinctly shows that a great external discrepancy of a localised form does not necessarily imply that there is also a peculiarity in the genital armature of the form.

c. *P. sarpedon adonarensis* from Adonara and Sambawa; f. 127.

The interesting external features of this form are pointed out by Mr. Rothschild on p. 324 of this volume. In pattern it comes near the subspecies from the neighbouring islands of Sumba, Timor, and Wetter; and we were rather surprised when we found that in the armature of the valve the specimens from Sambawa and Adonara disagree with those subspecies, and agree much better with the Indo-Malayan *sarpedon sarpedon*, as the dorsal ridge is dentate and has the transverse ridge as feebly developed as it normally is in Indian examples. F. 127 represents

Every individual specimen examined exhibited some peculiarity in the number, size, and form of the teeth of the dorsal ridge.

The lateral (ventral) fold (*h*) of the dorsal ridge (f. 98) is in f. 107 (Taiping, Malay Peninsula) absent, in f. 99 (Sikkim) very short, in f. 106 (Shan States) complete but very slightly raised, and is more distinct in f. 98 (Kumaon). In f. 100 (Sikkim) the fold runs up to a small tooth, which has a somewhat transverse position to the longitudinal ridge; in f. 108 the fold is raised to a low but obvious dentate ridge, which we shall call "*transverse ridge*."

In a Mindoro specimen caught by Mr. A. Everett in December 1894 the additional transverse ridge is raised above the level of the dorsal ridge, and forms a conspicuous, broad, tooth-like prominence; in f. 111 the dorsal ridge with the transverse prominence is represented in a view vertical upon the plane of the valve; and in f. 112 we give a view of the same organ from the apical side (with the eye a little above the valve).

Still more aberrant is a specimen from the Shan States caught by Mr. Roberts in the same district where the individual was obtained from which f. 106 is taken. The increase in the size of the transverse ridge, as illustrated by f. 107, 99, 106, 98, 100, 108, 111, and 112, reaches in f. 101 to 103 the maximum. The transverse ridge *h* is higher, strongly dentate, and more extended than the dentate portion of the dorsal ridge *d*: in f. 101 the organ is seen from above, in f. 102 from the ventral side, and in f. 103 from the apical side (compare f. 111 and 112).

We have examined more than a hundred specimens of *P. sarpedon sarpedon*, and found only one that has the additional transverse ridge so extraordinarily developed; the significance of this variation is obvious if we compare the special structure of the dorsal ridge of *P. sarpedon anthedon*, *milon*, *choredon*, *teredon*, etc. We shall have to refer to this particular case again.

b. *P. sarpedon semifasciatus* from China.

The Chinese subspecies of *sarpedon* is in the markings not always distinguishable from *sarpedon sarpedon*, but the greater number of the individuals from Central and Western China have a very remarkable character in the band of the hindwing being more or less obliterated. Such specimens with almost entirely black hindwings are, in respect to pattern, quantitatively more different from *sarpedon sarpedon* than the individuals of any other subspecies are. Though we dissected a long series of Chinese individuals, we did not perceive any character in the genital armature by which they could be differentiated from *sarpedon sarpedon*; and this concerns the examples which are most aberrant in pattern, as well as specimens with the ordinary *sarpedon sarpedon* pattern. The fact is of high interest, as it distinctly shows that a great external discrepancy of a localised form does not necessarily imply that there is also a peculiarity in the genital armature of the form.

c. *P. sarpedon adonarensis* from Adonara and Sambawa; f. 127.

The interesting external features of this form are pointed out by Mr. Rothschild on p. 324 of this volume. In pattern it comes near the subspecies from the neighbouring islands of Sumba, Timor, and Wetter; and we were rather surprised when we found that in the armature of the valve the specimens from Sambawa and Adonara disagree with those subspecies, and agree much better with the Indo-Malayan *sarpedon sarpedon*, as the dorsal ridge is dentate and has the transverse ridge as feebly developed as it normally is in Indian examples. F. 127 represents the dorsal ridge of an Adonara individual from the ventral side; it will be noticed that the dentate part of the ridge is markedly less extended than in *sarpedon sarpedon*, and that the transverse fold *h* has not developed to a ridge, as in f. 123 (Sumba), or f. 128 (Wetter) and f. 129 (Timor). The valve of *adonarensis* stands in shape intermediate between *sarpedon sarpedon* and *sarpedon jugans*, the lobes being slenderer than in the former, and shorter and broader than in the latter.

The individuals from the island of Lombok approach in external characters and in the genital armature still more the Indo-Malayan form.

d. *P. sarpedon teredon* from South India and Ceylon; f. 115 to 120, 133, 134.

The range of this subspecies is separated from that of *sarpedon sarpedon* by a wide area where most probably the species does not occur. We have examined above thirty specimens of *P. sarpedon teredon* from South India and Ceylon, all of which are in external features and in the genital armature well distinguishable from all other forms of *sarpedon*.

The valve is much narrower and the sinus considerably deeper than in *sarpedon sarpedon*. The ventral lobe (f. 115, 133, 134) is usually slender in its apical half, and curved towards the median axis of the abdomen, thus forming almost a hook-like organ ; the dorsal lobe is sometimes strongly pointed (f. 133). The inconstancy of the outline of the lobes is illustrated by f. 133 and 134, which are taken from South Indian individuals.

The ventral (longitudinal) portion of the valval fold extends farther towards the apex of the valve than in the preceding forms, and hence the ventri-dorsal portion has a more oblique direction. The dorsal ridge is much less raised than in *sarpedon sarpedon*; the denticulation is absent ; only the middle portion of the ridge, which corresponds to that part of the ridge of *sarpedon sarpedon* in f. 98 and 102 which bears the transverse fold or transverse ridge respectively, is elevated; it has, combined with the transverse fold (*h* of f. 98), developed in a vertical and transverse direction to a strong tooth-like transverse ridge, which slightly leans over basally and dorsally. As in f. 115, taken from an example from Trichopolis, the transverse ridge is too inconspicuous, we give an enlarged figure of the dorsal ridge of the same specimen in the same position (f. 116), and also a figure of the organ from the ventral side (f. 117). In f. 118 to 120 the transverse ridge alone is represented from the apical side ; mostly the ridge is shaped as in f. 119 ; its edge is usually not dentate, but there occur specimens, like that from which f. 118 (South India) is taken, which have the transverse ridge dentate ; in one of the Ceylonese examples (f. 120) the ridge is considerably smaller than in f. 119.

The individuals which belong to the ab. *thermodusa* have no character in the valve and its armature that is peculiar to them.

In external features and in the genital armature *teredon* comes much closer to the forms from the lesser Sunda Islands than to *sarpedon sarpedon*, which inhabits the interjacent countries.

e. *P. sarpedon jugans* from Sumba; f. 121 to 126.

"This form combines to a certain extent the characters of *sarpedon sarpedon* and *sarpedon timorensis*," and its "genital armature resembles more that of *timorensis* than that of *sarpedon* and *adonarensis*" (Rothschild, this volume, p. 324).

The sinus of the valve (f. 121) is deep. The ventral lobe is very slender, often the dorsal ridge of an Adonara individual from the ventral side; it will be noticed that the dentate part of the ridge is markedly less extended than in *sarpedon sarpedon*, and that the transverse fold *h* has not developed to a ridge, as in f. 123 (Sumba), or f. 128 (Wetter) and f. 129 (Timor). The valve of *adonarensis* stands in shape intermediate between *sarpedon sarpedon* and *sarpedon jugans*, the lobes being slenderer than in the former, and shorter and broader than in the latter.

The individuals from the island of Lombok approach in external characters and in the genital armature still more the Indo-Malayan form.

d. *P. sarpedon teredon* from South India and Ceylon; f. 115 to 120, 133, 134.

The range of this subspecies is separated from that of *sarpedon sarpedon* by a wide area where most probably the species does not occur. We have examined above thirty specimens of *P. sarpedon teredon* from South India and Ceylon, all of which are in external features and in the genital armature well distinguishable from all other forms of *sarpedon*.

The valve is much narrower and the sinus considerably deeper than in *sarpedon sarpedon*. The ventral lobe (f. 115, 133, 134) is usually slender in its apical half, and curved towards the median axis of the abdomen, thus forming almost a hook-like organ; the dorsal lobe is sometimes strongly pointed (f. 133). The inconstancy of the outline of the lobes is illustrated by f. 133 and 134, which are taken from South Indian individuals.

The ventral (longitudinal) portion of the valval fold extends farther towards the apex of the valve than in the preceding forms, and hence the ventri-dorsal portion has a more oblique direction. The dorsal ridge is much less raised than in *sarpedon sarpedon*; the denticulation is absent; only the middle portion of the ridge, which corresponds to that part of the ridge of *sarpedon sarpedon* in f. 98 and 102 which bears the transverse fold or transverse ridge respectively, is elevated; it has, combined with the transverse fold (*h* of f. 98), developed in a vertical and transverse direction to a strong tooth-like transverse ridge, which slightly leans over basally and dorsally. As in f. 115, taken from an example from Trichopolis, the transverse ridge is too inconspicuous, we give an enlarged figure of the dorsal ridge of the same specimen in the same position (f. 116), and also a figure of the organ from the ventral side (f. 117). In f. 118 to 120 the transverse ridge alone is represented from the apical side; mostly the ridge is shaped as in f. 119; its edge is usually not dentate, but there occur specimens, like that from which f. 118 (South India) is taken, which have the transverse ridge dentate; in one of the Ceylonese examples (f. 120) the ridge is considerably smaller than in f. 119.

The individuals which belong to the ab. *thermodusa* have no character in the valve and its armature that is peculiar to them.

In external features and in the genital armature *teredon* comes much closer to the forms from the lesser Sunda Islands than to *sarpedon sarpedon*, which inhabits the interjacent countries.

e. *P. sarpedon jugans* from Sumba; f. 121 to 126.

"This form combines to a certain extent the characters of *sarpedon sarpedon* and *sarpedon timorensis*," and its "genital armature resembles more that of *timorensis* than that of *sarpedon* and *adonarensis*" (Rothschild, this volume, p. 324).

The sinus of the valve (f. 121) is deep. The ventral lobe is very slender, often of almost rod-like appearance, sometimes even narrower than that of *sarpedon teredon*. The apex of the dorsal lobe is mostly rounded. The dorsal ridge is denticulate in the four specimens in the Tring Museum, but a comparison of f. 123 with f. 108 shows that the basal half of the ridge is very feebly raised; as in *teredon* (f. 117), the elevation is restricted to the median part of the ridge and the transverse ridge. F. 121, 122, 123, 125 are taken from the same individual: 122 and 123 give a view from the apical and ventral sides of the valve respectively, while f. 125 represents the median part of ridge alone in a view from above (as in f. 121). The dorsal ridge of another individual is represented from the apical side in f. 124; the transverse ridge is here much less developed than in the other specimen, in fact not more than in the Mindoro example represented by f. 112; the ridge *d* of the latter is, however, scarcely indicated in f. 124; the transverse ridge of f. 124 is enlarged in f. 126, which gives it in a view from above. The differences between f. 122 and 124, and 125 and 126, are very conspicuous.

f. *P. sarpedon timorensis* from Timor and Wetter; f. 128, 129.

We have only two specimens of this interesting form, one from Dili, Portuguese Timor, and the other from Wetter; the two individuals disagree somewhat with one another in external characters as well as in the form of the transverse ridge, but the differences are such that they may very well be individual and not subspecific.

The valve agrees with that of *jugans*, but the ventral lobe is less slender. The dorsal ridge, as in *teredon* from Ceylon and South India, is not denticulate; the transverse ridge is tooth-like, nearly as in *teredon*; f. 128 (Wetter) and 129 (Timor) represent the transverse ridge in a view from above: the figures may be compared with f. 125 and 126 (Sumba), 132 (Queensland), 138 (New Britain), 143 (Celebes), and 148 (Guadalcanar, Solomon Islands).

g. *P. sarpedon choredon* from Australia and New Guinea (including the islands near its coast); f. 130 to 132, 135 to 137.

The specimens from Waigeu and the northern parts of New Guinea are in external characters sometimes slightly different from ordinary individuals from Australia, and lead over to the next subspecies, which inhabits the Bismarck Archipelago.

The sinus of the valve is very deep (f. 135, Queensland). The ventral lobe is very prominent, its upper edge straight, its ventral (denticulate) edge evenly rounded; in breadth the ventral lobe is intermediate between *timorensis* and *jugans* on the one side, and *sarpedon sarpedon* on the other; in some examples the lobe is a third broader than in others. The dorsal lobe is in all examples we have seen rounded at the apex. The fold *e* of f. 135 is more curved than in *sarpedon sarpedon*, and takes about the same course as in *sarpedon teredon*.

The dorsal ridge divides basally in a dorsal (*r*) and a ventral (*s*) portion which correspond to the two slight folds marked *r* and *s* in f. 96. Now, in very many specimens both from Australia and New Guinea, only the ventral branch of the ridge participates in the formation of a high transverse ridge, as in f. 135 and in f. 136; the latter figure is taken from an individual from Redscar Bay, British New Guinea, and is a highly enlarged view of the transverse ridge and the adjoining parts of the dorsal ridge. In this case the dorsal ridge is rounded off, of almost rod-like appearance, sometimes even narrower than that of *sarpedon teredon*. The apex of the dorsal lobe is mostly rounded. The dorsal ridge is denticulate in the four specimens in the Tring Museum, but a comparison of f. 123 with f. 108 shows that the basal half of the ridge is very feebly raised; as in *teredon* (f. 117), the elevation is restricted to the median part of the ridge and the transverse ridge. F. 121, 122, 123, 125 are taken from the same individual: 122 and 123 give a view from the apical and ventral sides of the valve respectively, while f. 125 represents the median part of ridge alone in a view from above (as in f. 121). The dorsal ridge of another individual is represented from the apical side in f. 124; the transverse ridge is here much less developed than in the other specimen, in fact not more than in the Mindoro example represented by f. 112; the ridge *d* of the latter is, however, scarcely indicated in f. 124; the transverse ridge of f. 124 is enlarged in f. 126, which gives it in a view from above. The differences between f. 122 and 124, and 125 and 126, are very conspicuous.

f. *P. sarpedon timorensis* from Timor and Wetter; f. 128, 129.

We have only two specimens of this interesting form, one from Dili, Portuguese Timor, and the other from Wetter; the two individuals disagree somewhat with one another in external characters as well as in the form of the transverse ridge, but the differences are such that they may very well be individual and not subspecific.

The valve agrees with that of *jugans*, but the ventral lobe is less slender. The dorsal ridge, as in *teredon* from Ceylon and South India, is not denticulate; the transverse ridge is tooth-like, nearly as in *teredon*; f. 128 (Wetter) and 129 (Timor) represent the transverse ridge in a view from above: the figures may be compared with f. 125 and 126 (Sumba), 132 (Queensland), 138 (New Britain), 143 (Celebes), and 148 (Guadalcanar, Solomon Islands).

g. *P. sarpedon choredon* from Australia and New Guinea (including the islands near its coast); f. 130 to 132, 135 to 137.

The specimens from Waigeu and the northern parts of New Guinea are in external characters sometimes slightly different from ordinary individuals from Australia, and lead over to the next subspecies, which inhabits the Bismarck Archipelago.

The sinus of the valve is very deep (f. 135, Queensland). The ventral lobe is very prominent, its upper edge straight, its ventral (denticulate) edge evenly rounded; in breadth the ventral lobe is intermediate between *timorensis* and *jugans* on the one side, and *sarpedon sarpedon* on the other; in some examples the lobe is a third broader than in others. The dorsal lobe is in all examples we have seen rounded at the apex. The fold *e* of f. 135 is more curved than in *sarpedon sarpedon*, and takes about the same course as in *sarpedon teredon*.

The dorsal ridge divides basally in a dorsal (*r*) and a ventral (*s*) portion which correspond to the two slight folds marked *r* and *s* in f. 96. Now, in very many specimens both from Australia and New Guinea, only the ventral branch of the ridge participates in the formation of a high transverse ridge, as in f. 135 and in f. 136; the latter figure is taken from an individual from Redscar Bay, British New Guinea, and is a highly enlarged view of the transverse ridge and the adjoining parts of the dorsal ridge. In this case the dorsal ridge is rounded off, and has no teeth, except at the tip of the apical rod-like processus, which is longer than in all the preceding subspecies. F. 137 represents the dorsal ridge with the transverse ridge of a Redscar Bay individual in an apical view. Another extreme in the structure of the dorsal ridge is represented by f. 130 to 132, which are taken from an example from Cairns, North Queensland. F. 130 gives a view from the apical side ; the dorsal ridge *d* is provided with teeth, and the transverse ridge *h* is joined to the dorsal ridge, and is not a separate structure as in f. 136 ; f. 131 gives the ridges in a ventral view, while f. 132 is taken from above. The intergradations between the extremes figured here are equally abundant in Australia and New Guinea.

The individual variation of *choredon* in the direction from f. 130 to 137, from the transverse ridge forming one piece with the dorsal ridge (as in *sarpedon sarpedon, teredon, jugans*), to the other extreme where the transverse ridge stands isolated, will serve to comprehend the still more exaggerated development of the transverse ridge in some of the following subspecies.

h. *P. sarpedon imparilis* from New Britain ; f. 138.

The external differences between this subspecies and the preceding one, though slight, are prominent enough to enable us to distinguish all our New Britain individuals from *choredon*. In the genital armature *imparilis* comes again very close to *choredon* ; the lobes of the valve are, however, more pointed (f. 138) ; the transverse ridge is smaller, stands less oblique, and leans over towards the base of the valve ; the dentition of the transverse ridge is as variable as in *choredon*.

The specimens with additional spots on the forewing have no character in the valve and the armature peculiar to them.

i. *P. sarpedon impar* from New Georgia, Solomon Islands.

The *male* of this insect is unknown; the *female* is in pattern midway between the preceding and the following form.

k. *P. sarpedon isander* from Guadalcanar and Bougainville, Solomon Islands: f. 148.

Though this form is so very aberrant in markings that it has been described by Godman & Salvin as a distinct species, and has also been kept separate from *sarpedon* by Mr. Rothschild in his Revision (who, however, informs me now that, in consequence of the receipt of more specimens, he must sink it to the rank of a subspecies of *sarpedon*), the valve and its armature are only slightly different from that of *imparilis*. The ventral lobe of the valve is broader, blunter, and shorter. The transverse ridge is not separated from the dorsal ridge ; it is high, mostly simple, and seldom notched or faintly dentate. F. 148 is taken from an individual from Guadalcanar.

l. *P. sarpedon dodingensis* from the Northern Moluccas (Halmaheira and Batjan); f. 139 and 140.

The sinus of the valve (f. 139) is very deep and especially narrow, being about twice as deep as broad. The ventral lobe of the valve is shaped nearly as in *imparilis*. The dorsal ridge is bifurcate as in *choredon*, but the bifurcation takes place not far from the apex of the valve; the ventral part of the ridge is raised and forms the usual transverse ridge. From f. 140, which is taken from the same and has no teeth, except at the tip of the apical rod-like processus, which is longer than in all the preceding subspecies. F. 137 represents the dorsal ridge with the transverse ridge of a Redscar Bay individual in an apical view. Another extreme in the structure of the dorsal ridge is represented by f. 130 to 132, which are taken from an example from Cairns, North Queensland. F. 130 gives a view from the apical side; the dorsal ridge *d* is provided with teeth, and the transverse ridge *h* is joined to the dorsal ridge, and is not a separate structure as in f. 136; f. 131 gives the ridges in a ventral view, while f. 132 is taken from above. The intergradations between the extremes figured here are equally abundant in Australia and New Guinea.

The individual variation of *choredon* in the direction from f. 130 to 137, from the transverse ridge forming one piece with the dorsal ridge (as in *sarpedon sarpedon*, *teredon*, *jugans*), to the other extreme where the transverse ridge stands isolated, will serve to comprehend the still more exaggerated development of the transverse ridge in some of the following subspecies.

h. *P. sarpedon imparilis* from New Britain; f. 138.

The external differences between this subspecies and the preceding one, though slight, are prominent enough to enable us to distinguish all our New Britain individuals from *choredon*. In the genital armature *imparilis* comes again very close to *choredon*; the lobes of the valve are, however, more pointed (f. 138); the transverse ridge is smaller, stands less oblique, and leans over towards the base of the valve; the dentition of the transverse ridge is as variable as in *choredon*.

The specimens with additional spots on the forewing have no character in the valve and the armature peculiar to them.

i. *P. sarpedon impar* from New Georgia, Solomon Islands.

The *male* of this insect is unknown; the *female* is in pattern midway between the preceding and the following form.

k. *P. sarpedon isander* from Guadalcanar and Bougainville, Solomon Islands; f. 148.

Though this form is so very aberrant in markings that it has been described by Godman & Salvin as a distinct species, and has also been kept separate from *sarpedon* by Mr. Rothschild in his Revision (who, however, informs me now that, in consequence of the receipt of more specimens, he must sink it to the rank of a subspecies of *sarpedon*), the valve and its armature are only slightly different from that of *imparilis*. The ventral lobe of the valve is broader, blunter, and shorter. The transverse ridge is not separated from the dorsal ridge; it is high, mostly simple, and seldom notched or faintly dentate. F. 148 is taken from an individual from Guadalcanar.

l. *P. sarpedon dodingensis* from the Northern Moluccas (Halmaheira and Batjan); f. 139 and 140.

The sinus of the valve (f. 139) is very deep and especially narrow, being about twice as deep as broad. The ventral lobe of the valve is shaped nearly as in *imparilis*. The dorsal ridge is bifurcate as in *choredon*, but the bifurcation takes place not far from the apex of the valve; the ventral part of the ridge is raised and forms the usual transverse ridge. From f. 140, which is taken from the same specimen as f. 139 and gives a view of the dorsal ridge from the apical side, it will be observed that the dentate ridge differs essentially from the transverse ridge of f. 103, 130, 137, 142, 144, in so far as it is not homologous to the fold *h* of f. 98, but to the middle portion of the dentate dorsal ridge to which that fold is joined. In a Batjan example the ridge, which in f. 140 is tridentate, is much reduced. The apical process of the dorsal ridge is long.

m. *P. sarpedon anthedon* from the Southern Moluccas (Amboina, Ceram); f. 141 and 142.

The sinus of the valve is twice as broad as in *sarpedon dodingensis*, but not so deep as in that form. The ventral lobe of the valve varies a good deal individually, and has generally the outline of that of *choredon* or *dodingensis* ; the dorsal lobe is broader than the ventral one, and rounded at the apex. The dorsal ridge has the apical (rod-like) process prolonged, as is the case in *dodingensis*. The transverse ridge is always strongly developed, and nearly always so obviously detached as in f. 142, which is taken from a Ceram individual of which f. 141 represents the valve and harpe from above.

In external features *anthedon* is much more closely allied with *dodingensis* than with *choredon*; in the valve and its armature the difference between the former is, on the contrary, much greater than that between *anthedon* and *choredon*. *Anthedon* is distinguished from *choredon* only in the free apical process of the dorsal ridge being longer, and in the transverse ridge leaning more evidently over basally, as will be seen from comparing f. 135 and 141, and 137 and 142; while it differs from *dodingensis* in having a broader dorsal lobe, a much wider sinus, and a differently shaped and differently situate transverse ridge. The relationship indicated by pattern is therefore not the same as that which we must deduce from the structure of the genital armature.

n. *P. sarpedon monticolus* from Bonthain Peak, S. Celebes ; f. 146 and 147.

The discovery of a mountain form of *sarpedon* in Celebes which is in general appearance very different from the form inhabiting the lower districts of the island is highly interesting. The subspecies resembles on superficial examination Indo-Malayan individuals of *sarpedon sarpedon* ; the actual affinities of the subspecies are, in respect to the external characters, as follows: In the green colour of the markings *monticolus*—it ought to be *monticola!*—agrees with *sarpedon sarpedon*, *sarpedon jugans*, *sarpedon adonarensis*, and *sarpedon timorensis*, and differs conspicuously from its compatriot *milon* and the Moluccan races. In the shape of the wings it resembles *sarpedon sarpedon* from the Sunda Islands. In the shape of the median band of the forewing it comes nearest to *sarpedon dodingensis* from the Northern Moluccas, except in the third spot being larger than the fourth, in which character it agrees with *timorensis*. The underside of the hindwing is in *monticolus*, *milon* (Celebes), and *dodingensis* (Northern Moluccas), in opposition to all other subspecies, provided with a red mark before the median cell between veins 6 and 7. And, lastly, the genital armature of *monticolus* stands intermediate in structure between that of *milon* and that of *dodingensis*, and hence is obviously different from that of *sarpedon sarpedon*.

We have to lay great stress upon the mixture of characters found in *P. sarpedon monticolus*. As the relationship to *milon* from Celebes, *sarpedon* from the Sunda Islands, and *dodingensis* from the Northern Moluccas is equally great in the specimen as f. 139 and gives a view of the dorsal ridge from the apical side, it will be observed that the dentate ridge differs essentially from the transverse ridge of f. 103, 130, 137, 142, 144, in so far as it is not homologous to the fold *h* of f. 98, but to the middle portion of the dentate dorsal ridge to which that fold is joined. In a Batjan example the ridge, which in f. 140 is tridentate, is much reduced. The apical process of the dorsal ridge is long.

m. *P. sarpedon anthedon* from the Southern Moluccas (Amboina, Ceram); f. 141 and 142.

The sinus of the valve is twice as broad as in *sarpedon dodingensis*, but not so deep as in that form. The ventral lobe of the valve varies a good deal individually, and has generally the outline of that of *choredon* or *dodingensis* ; the dorsal lobe is broader than the ventral one, and rounded at the apex. The dorsal ridge has the apical (rod-like) process prolonged, as is the case in *dodingensis.* The transverse ridge is always strongly developed, and nearly always so obviously detached as in f. 142, which is taken from a Ceram individual of which f. 141 represents the valve and harpe from above.

In external features *anthedon* is much more closely allied with *dodingensis* than with *choredon*; in the valve and its armature the difference between the former is, on the contrary, much greater than that between *anthedon* and *choredon. Anthedon* is distinguished from *choredon* only in the free apical process of the dorsal ridge being longer, and in the transverse ridge leaning more evidently over basally, as will be seen from comparing f. 135 and 141, and 137 and 142; while it differs from *dodingensis* in having a broader dorsal lobe, a much wider sinus, and a differently shaped and differently situate transverse ridge. The relationship indicated by pattern is therefore not the same as that which we must deduce from the structure of the genital armature.

n. *P. sarpedon monticolus* from Bonthain Peak, S. Celebes ; f. 146 and 147.

The discovery of a mountain form of *sarpedon* in Celebes which is in general appearance very different from the form inhabiting the lower districts of the island is highly interesting. The subspecies resembles on superficial examination Indo-Malayan individuals of *sarpedon sarpedon* ; the actual affinities of the subspecies are, in respect to the external characters, as follows: In the green colour of the markings *monticolus*—it ought to be *monticola!*—agrees with *sarpedon sarpedon*, *sarpedon jugans*, *sarpedon adonarensis*, and *sarpedon timorensis*, and differs conspicuously from its compatriot *milon* and the Moluccan races. In the shape of the wings it resembles *sarpedon sarpedon* from the Sunda Islands. In the shape of the median band of the forewing it comes nearest to *sarpedon dodingensis* from the Northern Moluccas, except in the third spot being larger than the fourth, in which character it agrees with *timorensis.* The underside of the hindwing is in *monticolus*, *milon* (Celebes), and *dodingensis* (Northern Moluccas), in opposition to all other subspecies, provided with a red mark before the median cell between veins 6 and 7. And, lastly, the genital armature of *monticolus* stands intermediate in structure between that of *milon* and that of *dodingensis*, and hence is obviously different from that of *sarpedon sarpedon.*

We have to lay great stress upon the mixture of characters found in *P. sarpedon monticolus.* As the relationship to *milon* from Celebes, *sarpedon* from the Sunda Islands, and *dodingensis* from the Northern Moluccas is equally great in the characters of the wing and valve, we have no reason whatever to say that *monticolus* is derived from *sarpedon sarpedon*, or from *sarpedon dodingensis*, and not from *sarpedon milon*; and hence a conclusion, based upon the occurrence of a special form of *P. sarpedon* on Bonthain Peak, as to the probable geological history of Celebes—connection with the Sunda Islands or with the Northern Moluccas—would lack the necessary facts. We shall have to refer again to *monticolus* in the last chapter of this paper.

The valve is nearly shaped as in *sarpedon milon*, *i.e.* the ventral lobe is much longer and narrower than in *sarpedon sarpedon*. The dorsal ridge (f. 146, from apical side) bears a transverse dentate ridge, similar in position to that of *dodingensis* (f. 140), but differently shaped; the dentate ridge is much less extended than in ordinary examples of *milon* (f. 144). F. 146 gives a dorsal view of the ridge.

o. *P. sarpedon milon* from Celebes, the Sulla Islands, and the island of Talaut; f. 143, 144, and 145.

This long-winged and narrow-banded subspecies has the blue colour of the wing-band in common with the Moluccan races; the nearest ally in respect to the pattern of the wing is *dodingensis*, which has, like *milon* and *monticolus*, an additional red spot before the cell on the underside of the hindwing, and has the median band of both wings also obviously narrower than it is in the subspecies from Amboina and Ceram.

The sinus of the valve of *milon* (f. 143) is deep and broad; the ventral lobe of the valve is very slender and long, resembling somewhat that of *jugans* from Sumba (f. 121) and *teredon* from Ceylon and S. India (f. 133). The apical processus of the dorsal ridge is nearly as long as in the two Moluccan races. The transverse ridge has developed to a broad saw-like organ, which when seen from above sometimes almost extends to the sinus of the valve. In the ventral view of the dorsal ridge (f. 145, Celebes specimen) the denticulate portion of the dorsal ridge itself (*d*) is plainly visible; this portion of the ridge is not developed in the Moluccan races, but in *monticolus* from Bonthain Peak (f. 147). The transverse ridge (*h*) is in this specimen almost perpendicular. A view of the same organ from the apical side of the valve is given in f. 144; the ridge is larger than in any other subspecies, but there is some individual variation in the size of the ridge.

We have only one ♂ from the island of Mangiola (Sulla Islands), which, like the *female*, differs from the Celebes individuals in having a narrower median band to the wings. The valve and its armature is in this ♂ very slightly different from that of our Celebes examples; but, of course, we cannot tell from one individual whether the difference is due to individual or to local variation.

The more prominent facts of variation illustrated by f. 96 to 148 are as follows:—

(1) The genital armature varies according to locality: the Chinese subspecies agrees in the apparatus, however, with the Indo-Malayan one, in spite of very prominent external differences.

(2) The distinguishing characters in the genital armature of the subspecies are found in the valve as well as in the harpe.

(3) The individual variation within the Indo-Malayan subspecies, of which a large material has been examined, is so great that the difference between every two nearest allied subspecies is small compared with the difference exhibited by the extreme individuals of the Indo-Malayan subspecies.

characters of the wing and valve, we have no reason whatever to say that *monticolus* is derived from *sarpedon sarpedon*, or from *sarpedon dodingensis*, and not from *sarpedon milon*; and hence a conclusion, based upon the occurrence of a special form of *P. sarpedon* on Bonthain Peak, as to the probable geological history of Celebes—connection with the Sunda Islands or with the Northern Moluccas—would lack the necessary facts. We shall have to refer again to *monticolus* in the last chapter of this paper.

The valve is nearly shaped as in *sarpedon milon*, *i.e.* the ventral lobe is much longer and narrower than in *sarpedon sarpedon*. The dorsal ridge (f. 146, from apical side) bears a transverse dentate ridge, similar in position to that of *dodingensis* (f. 140), but differently shaped; the dentate ridge is much less extended than in ordinary examples of *milon* (f. 144). F. 146 gives a dorsal view of the ridge.

o. *P. sarpedon milon* from Celebes, the Sulla Islands, and the island of Talaut; f. 143, 144, and 145.

This long-winged and narrow-banded subspecies has the blue colour of the wing-band in common with the Moluccan races; the nearest ally in respect to the pattern of the wing is *dodingensis*, which has, like *milon* and *monticolus*, an additional red spot before the cell on the underside of the hindwing, and has the median band of both wings also obviously narrower than it is in the subspecies from Amboina and Ceram.

The sinus of the valve of *milon* (f. 143) is deep and broad; the ventral lobe of the valve is very slender and long, resembling somewhat that of *jugans* from Sumba (f. 121) and *teredon* from Ceylon and S. India (f. 133). The apical processus of the dorsal ridge is nearly as long as in the two Moluccan races. The transverse ridge has developed to a broad saw-like organ, which when seen from above sometimes almost extends to the sinus of the valve. In the ventral view of the dorsal ridge (f. 145, Celebes specimen) the denticulate portion of the dorsal ridge itself (*d*) is plainly visible; this portion of the ridge is not developed in the Moluccan races, but in *monticolus* from Bonthain Peak (f. 147). The transverse ridge (*h*) is in this specimen almost perpendicular. A view of the same organ from the apical side of the valve is given in f. 144; the ridge is larger than in any other subspecies, but there is some individual variation in the size of the ridge.

We have only one ♂ from the island of Mangiola (Sulla Islands), which, like the *female*, differs from the Celebes individuals in having a narrower median band to the wings. The valve and its armature is in this ♂ very slightly different from that of our Celebes examples; but, of course, we cannot tell from one individual whether the difference is due to individual or to local variation.

The more prominent facts of variation illustrated by f. 96 to 148 are as follows:—

(1) The genital armature varies according to locality: the Chinese subspecies agrees in the apparatus, however, with the Indo-Malayan one, in spite of very prominent external differences.

(2) The distinguishing characters in the genital armature of the subspecies are found in the valve as well as in the harpe.

(3) The individual variation within the Indo-Malayan subspecies, of which a large material has been examined, is so great that the difference between every two nearest allied subspecies is small compared with the difference exhibited by the extreme individuals of the Indo-Malayan subspecies.

(4) The Ceylonese and South Indian subspecies is in the genital armature and in the shape of the wing nearer related * to the forms inhabiting Sumba, Wetter, and Timor, than to the Indian form.

(5) The subspecies which are in colour and pattern nearly allied * (*sarpedon sarpedon* from India, *sarpedon choredon* from Australia, *sarpedon monticolus* from Celebes) need not be similar in respect to the genital armature.

(6) The spring and summer broods in North India and Japan are not different in the genital armature.

11. **Papilio bathycles** ; f. 46 to 50.

We have selected this species out of a number of "green" Eastern Papilios for two reasons : first, because the harpe of the species has long spines and processes the variation of which is more easily demonstrated ; secondly, because the three subspecies of the species (Java ; Malacca, Sumatra, Borneo ; North India and Burma), though in external characters not always distinguishable (at least as regards those two of them of which we have a long series), are in the harpes, according to our material, always different. We believe that the great gap between the harpe of the North Indian form and that of the Malayan form, and the smaller gap between the Malayan and the Java subspecies, are due to the circumstance that we have not examined specimens from the interjacent countries, Tenasserim and South-West Sumatra.

As the valve of *P. bathycles* does not vary to any extent, we figure only the harpe. The harpe consists of a fold extending ventrally from the base of the valve to near the apex, and from here to near the dorsal edge of the valve ; the fold is apically produced into a ventral spine (*a*), a ventral ridge (*b*), and into a dorsal ridge (*c*), all of which extend in an apical direction; the fold between the dorsal ridge and the ventral ridge is very slightly raised.

a. *P. bathycles bathycles* from Java ; f. 46.

We have examined but four individuals, the harpe of one of which is represented by f. 46. In all four specimens the ventral spine (*a*) is simple, without denticulation ; the ventral ridge is dentate, either of the form as represented in f. 46, with a small dentate dilatation at its dorsal edge, or the place of this dilatation is occupied by some small teeth ; the dorsal ridge is broad, denticulate, and has generally one larger tooth, as in f. 46 ; the surface of the ridge is basally limited by a faint fold.

b. *P. bathycles bathycloides* from Sumatra, Malacca, and Borneo ; f. 47.

F. 47 is taken from a Bornean example. The ventral spine is either simple, or, as in figure, denticulate at the tip ; the ventral ridge is longer and basally much narrower than in the Java form, being there without dilatation or denticulation ; the dorsal ridge is nearly shaped as in *bathycles bathycles*, but the fold *e* is more obviously marked and has a different direction.

c. *P. bathycles chiron* from Sikkim, Assam, Burma ; f. 48, 49, 50.

The material of this form which stood at our disposal was much larger than that of the two preceding subspecies, and consequently the amount of variability

---

* The words "allied" and "related" mean here simply "similarity," not phylogenetic relationship.

(4) The Ceylonese and South Indian subspecies is in the genital armature and in the shape of the wing nearer related * to the forms inhabiting Sumba, Wetter, and Timor, than to the Indian form.

(5) The subspecies which are in colour and pattern nearly allied * (*sarpedon sarpedon* from India, *sarpedon choredon* from Australia, *sarpedon monticolus* from Celebes) need not be similar in respect to the genital armature.

(6) The spring and summer broods in North India and Japan are not different in the genital armature.

11. **Papilio bathycles** ; f. 46 to 50.

We have selected this species out of a number of "green" Eastern Papilios for two reasons: first, because the harpe of the species has long spines and processes the variation of which is more easily demonstrated; secondly, because the three subspecies of the species (Java; Malacca, Sumatra, Borneo; North India and Burma), though in external characters not always distinguishable (at least as regards those two of them of which we have a long series), are in the harpes, according to our material, always different. We believe that the great gap between the harpe of the North Indian form and that of the Malayan form, and the smaller gap between the Malayan and the Java subspecies, are due to the circumstance that we have not examined specimens from the interjacent countries, Tenasserim and South-West Sumatra.

As the valve of *P. bathycles* does not vary to any extent, we figure only the harpe. The harpe consists of a fold extending ventrally from the base of the valve to near the apex, and from here to near the dorsal edge of the valve; the fold is apically produced into a ventral spine (*a*), a ventral ridge (*b*), and into a dorsal ridge (*c*), all of which extend in an apical direction; the fold between the dorsal ridge and the ventral ridge is very slightly raised.

a. *P. bathycles bathycles* from Java ; f. 46.

We have examined but four individuals, the harpe of one of which is represented by f. 46. In all four specimens the ventral spine (*a*) is simple, without denticulation; the ventral ridge is dentate, either of the form as represented in f. 46, with a small dentate dilatation at its dorsal edge, or the place of this dilatation is occupied by some small teeth; the dorsal ridge is broad, denticulate, and has generally one larger tooth, as in f. 46; the surface of the ridge is basally limited by a faint fold.

b. *P. bathycles bathycloides* from Sumatra, Malacca, and Borneo ; f. 47.

F. 47 is taken from a Bornean example. The ventral spine is either simple, or, as in figure, denticulate at the tip; the ventral ridge is longer and basally much narrower than in the Java form, being there without dilatation or denticulation; the dorsal ridge is nearly shaped as in *bathycles bathycles*, but the fold *e* is more obviously marked and has a different direction.

c. *P. bathycles chiron* from Sikkim, Assam, Burma ; f. 48, 49, 50.

The material of this form which stood at our disposal was much larger than that of the two preceding subspecies, and consequently the amount of variability observed in *chiron* greater than the amount observed in *bathycloides* and *bathycles*. As in wing-pattern *bathycloides* and *chiron* are not always distinguishable with certainty, while *bathycles* is more easily recognisable, the dissimilarity in the harpes of *bathycloides* and *chiron* is much greater than the difference between the harpes of *bathycloides* and *bathycles*. Comparing f. 46 (*bathycles*) and 47 (*bathycloides*) with f. 48 to 50, which represent *chiron*, we observe as main character of the harpe of *chiron* that the dorsal ridge (*c*) is reduced to a small triangular tooth. Besides, the dorsal tooth *c* stands nearer the ventral ridge owing to an increase in breadth of the ventral portion of the harpe; the ventral spine has a somewhat different direction, and the ventral ridge is differently shaped.

---

* The words "allied" and "related" mean here simply "similarity," not phylogenetic relationship.

The division of the ventral ridge of *bathycles* into two lobes (f. 46) is in f. 48, taken from a Shillong (Assam) example, more obvious; in f. 49 (Sikkim) the bifurcation is complete and the denticulation is much reduced: in an individual from the Shan States (f. 50) the ridge is divided into three teeth.

The ventral spine is either simple (f. 49), or denticulate at the tip.

The dorsal, triangular, ridge varies a good deal in size, but to our knowledge this variation is independent of locality, as is also the variation of the ventral ridge and ventral spine of *chiron*.

There often occur specimens of *chiron* in which the ochreous costal mark on the underside of the hindwing is wanting (ab. *chironides*), a character by which also *bathycloides* is distinguished from *bathycles*; in the genital armature of ab. *chironides* there is no peculiarity, and we also failed to find any distinguishing character in the genital armature of the spring specimens from Sikkim (broad-banded) as compared with the summer specimens (narrow-banded).

The facts of variation illustrated by f. 46 to 50 are as follows:—

(1) The three subspecies of *P. bathycles*, the Javan (*bathycles*), the Malayan (*bathycloides*), and the Indian (*chiron*), have the harpe built up after the same plan, but the detail of the structure furnishes in the specimens examined obvious distinguishing characters.

(2) The Malayan and the Indian forms are nearest related in pattern, while the Malayan and the Javan forms are nearest related in the structure of the harpe.

(3) The individuals of the spring and summer broods of *chiron*, and the specimens of *chiron* ab. *chiron* and *chiron* ab. *chironides*, are in the genital armature the same.

12. **Papilio aristeus**; f. 72 to 83.

This species ranges from Sikkim all over the Indo-Australian Archipelago, and is replaced on Celebes and some islands south of it by a close ally (*P. rhesus*), and on the islands of the Bismarck Archipelago by another close ally (*P. paron*). Mr. Rothschild, Nov. Zool. 1895. p. 418, distinguishes four subspecies, which, arranged according to the geographical position of the district which each of them inhabits, are as follows:—

(1) *P. aristeus anticrates* in Northern India (Sikkim and Assam).

(2) *P. aristeus hermocrates* from Upper Burma to Timor and the Philippine Islands.

(3) *P. aristeus aristeus* on the Moluccas.

(4) *P. aristeus parmatus* in Queensland, on New Guinea and Waigeu.

observed in *chiron* greater than the amount observed in *bathycloides* and *bathycles*. As in wing-pattern *bathycloides* and *chiron* are not always distinguishable with certainty, while *bathycles* is more easily recognisable, the dissimilarity in the harpes of *bathycloides* and *chiron* is much greater than the difference between the harpes of *bathycloides* and *bathycles*. Comparing f. 46 (*bathycles*) and 47 (*bathycloides*) with f. 48 to 50, which represent *chiron*, we observe as main character of the harpe of *chiron* that the dorsal ridge (*c*) is reduced to a small triangular tooth. Besides, the dorsal tooth *c* stands nearer the ventral ridge owing to an increase in breadth of the ventral portion of the harpe; the ventral spine has a somewhat different direction, and the ventral ridge is differently shaped.

The division of the ventral ridge of *bathycles* into two lobes (f. 46) is in f. 48, taken from a Shillong (Assam) example, more obvious; in f. 49 (Sikkim) the bifurcation is complete and the denticulation is much reduced: in an individual from the Shan States (f. 50) the ridge is divided into three teeth.

The ventral spine is either simple (f. 49), or denticulate at the tip.

The dorsal, triangular, ridge varies a good deal in size, but to our knowledge this variation is independent of locality, as is also the variation of the ventral ridge and ventral spine of *chiron*.

There often occur specimens of *chiron* in which the ochreous costal mark on the underside of the hindwing is wanting (ab. *chironides*), a character by which also *bathycloides* is distinguished from *bathycles*; in the genital armature of ab. *chironides* there is no peculiarity, and we also failed to find any distinguishing character in the genital armature of the spring specimens from Sikkim (broad-banded) as compared with the summer specimens (narrow-banded).

The facts of variation illustrated by f. 46 to 50 are as follows:—

(1) The three subspecies of *P. bathycles*, the Javan (*bathycles*), the Malayan (*bathycloides*), and the Indian (*chiron*), have the harpe built up after the same plan, but the detail of the structure furnishes in the specimens examined obvious distinguishing characters.

(2) The Malayan and the Indian forms are nearest related in pattern, while the Malayan and the Javan forms are nearest related in the structure of the harpe.

(3) The individuals of the spring and summer broods of *chiron*, and the specimens of *chiron* ab. *chiron* and *chiron* ab. *chironides*, are in the genital armature the same.

12. **Papilio aristeus**; f. 72 to 83.

This species ranges from Sikkim all over the Indo-Australian Archipelago, and is replaced on Celebes and some islands south of it by a close ally (*P. rhesus*), and on the islands of the Bismarck Archipelago by another close ally (*P. paron*). Mr. Rothschild, Nov. Zool. 1895. p. 418, distinguishes four subspecies, which, arranged according to the geographical position of the district which each of them inhabits, are as follows:—

(1) *P. aristeus anticrates* in Northern India (Sikkim and Assam).

(2) *P. aristeus hermocrates* from Upper Burma to Timor and the Philippine Islands.

(3) *P. aristeus aristeus* on the Moluccas.

(4) *P. aristeus parmatus* in Queensland, on New Guinea and Waigeu.

That these four forms are really one species there can scarcely be any doubt, for the distinguishing characters are by no means perfectly constant.

P. aristeus, rhesus, paron, antiphates, etc., and all the green Eastern Papilios have in neuration a prominent character in common: in all of them the first subcostal branch is *invariably* anastomosed to the costal nervure. The relationship indicated by this phenomenon is doubtless blood-relationship, not simply form-relationship, as the structure of the larvae, pupae, and the morphology of the imagines point in the same direction. The form of the ninth abdominal segment in the *male*, and especially that of the eighth in the *female*, is in several groups of Indian Papilios with that peculiarity in the neuration morphologically similar, while those segments are in *P. podalirius, ajax*, and allies, which have a superficial resemblance to *aristeus, antiphates*, etc., of quite a different form (compare f. 181, *podalirius* ♀, and 182, *sarpedon* ♀).

The peculiar form of the valve of *P. aristeus* will easily be understood if one compares with f. 72 (*aristeus anticrates*) the valve of *P. sarpedon* (f. 96).

The apical sinus which in *sarpedon* occupies the middle of the apex is in *aristeus* more dorsal and is very narrow; in a view perpendicular on the plane of the valve, as in f. 72, the sinus is concealed by a brush-like organ (*b*); but in f. 75, which represents the brush-like organ from the ventral side (*minus* the bristles), the narrow sinus between *a* and *b* is visible.

The organ *b* is homologous to the dorsal lobe of the valve of *sarpedon*, and therefore will here be called so. The ventral lobe of the valve (*a*) is very broad and rounded, or somewhat triangular. The position of the two lobes against one another can easily be imitated with the thumb (representing the dorsal lobe) and the four other fingers (representing the ventral lobe) by moving the thumb inwards.

The middle portion of the inner edge of the thick and raised ventral margin of the valve is furnished with short bristles.

The armature of the valve is also homologous to that of *sarpedon*. The usual fold of the inner sheath begins ventrally at the base of the valve, is soon curved a little dorsally, and then suddenly raised into a strongly chitinised, denticulate, ridge (*e*); from here the fold turns dorsally and becomes soon dilated into a long process (*c*), the subapical tooth of *sarpedon*, which we shall call *subapical process*; this process leans strongly over dorsally and apically, is curved, and penetrates between the dorsal and ventral lobe of the valve, so that its tip is visible when the valve is viewed from the dorsal side. The position of the subdorsal process will become clear from f. 75 and 82.

The variation according to individuals and according to locality affects the dorsal lobe (*b*), the ventral denticulate ridge (*e*), and the subdorsal process (*c*).

a. *P. aristeus anticrates* from Sikkim and Assam; f. 72, 73, 75.

The dorsal lobe of the valve is always very broad; its free apical portion is ovate. The outline is not always the same: sometimes the lobe is a little slenderer than in f. 75, which represents the average form and is taken from a Sikkim example; sometimes it is a little shorter.

The ventral ridge appears in the view from above (f. 72, Sikkim individual) almost straight; the ridge is concave dorsally, its middle portion being more ventral than the basal and apical edge. When seen from the dorsal side (f. 73) the denticulation of the ridge is more prominent; in all specimens examined

That these four forms are really one species there can scarcely be any doubt, for the distinguishing characters are by no means perfectly constant.

P. aristeus, *rhesus*, *paron*, *antiphates*, etc., and all the green Eastern Papilios have in neuration a prominent character in common: in all of them the first subcostal branch is *invariably* anastomosed to the costal nervure. The relationship indicated by this phenomenon is doubtless blood-relationship, not simply form-relationship, as the structure of the larvae, pupae, and the morphology of the imagines point in the same direction. The form of the ninth abdominal segment in the *male*, and especially that of the eighth in the *female*, is in several groups of Indian Papilios with that peculiarity in the neuration morphologically similar, while those segments are in *P. podalirius*, *ajax*, and allies, which have a superficial resemblance to *aristeus*, *antiphates*, etc., of quite a different form (compare f. 181, *podalirius* ♀, and 182, *sarpedon* ♀).

The peculiar form of the valve of *P. aristeus* will easily be understood if one compares with f. 72 (*aristeus anticrates*) the valve of *P. sarpedon* (f. 96).

The apical sinus which in *sarpedon* occupies the middle of the apex is in *aristeus* more dorsal and is very narrow; in a view perpendicular on the plane of the valve, as in f. 72, the sinus is concealed by a brush-like organ (*b*); but in f. 75, which represents the brush-like organ from the ventral side (*minus* the bristles), the narrow sinus between *a* and *b* is visible.

The organ *b* is homologous to the dorsal lobe of the valve of *sarpedon*, and therefore will here be called so. The ventral lobe of the valve (*a*) is very broad and rounded, or somewhat triangular. The position of the two lobes against one another can easily be imitated with the thumb (representing the dorsal lobe) and the four other fingers (representing the ventral lobe) by moving the thumb inwards.

The middle portion of the inner edge of the thick and raised ventral margin of the valve is furnished with short bristles.

The armature of the valve is also homologous to that of *sarpedon*. The usual fold of the inner sheath begins ventrally at the base of the valve, is soon curved a little dorsally, and then suddenly raised into a strongly chitinised, denticulate, ridge (*e*); from here the fold turns dorsally and becomes soon dilated into a long process (*c*), the subapical tooth of *sarpedon*, which we shall call *subapical process*; this process leans strongly over dorsally and apically, is curved, and penetrates between the dorsal and ventral lobe of the valve, so that its tip is visible when the valve is viewed from the dorsal side. The position of the subdorsal process will become clear from f. 75 and 82.

The variation according to individuals and according to locality affects the dorsal lobe (*b*), the ventral denticulate ridge (*e*), and the subdorsal process (*c*).

a. *P. aristeus anticrates* from Sikkim and Assam; f. 72, 73, 75.

The dorsal lobe of the valve is always very broad; its free apical portion is ovate. The outline is not always the same: sometimes the lobe is a little slenderer than in f. 75, which represents the average form and is taken from a Sikkim example; sometimes it is a little shorter.

The ventral ridge appears in the view from above (f. 72, Sikkim individual) almost straight; the ridge is concave dorsally, its middle portion being more ventral than the basal and apical edge. When seen from the dorsal side (f. 73) the denticulation of the ridge is more prominent; in all specimens examined the longest, most basal, tooth (right-hand side in figure) is nearly horizontal. The subdorsal process is simple, without denticulation.

There is no difference in the genital armature between the darker and the less dark specimens from Sikkim and Assam.

b. *P. aristeus hermocrates* from Burma to Timor, Borneo, Palawan, and the Philippine Islands; f. 74, 76 to 80.

We have examined individuals from the Shan States, Borneo, Palawan, the Philippine Islands, Sumba, Kalao, Wetter, and Timor. The individual variation in the pattern of the wings and in the size of the specimens is considerable, but we cannot find distinguishing characters which would necessitate a division of *hermocrates* into more subspecies; the Wetter and Timor individuals, from which islands we have only three altogether, are faintly different in the shape of the forewing, and may perhaps, on receipt of more material, be separable from *hermocrates*. An examination of the genital armature likewise did not furnish us with characters by which specimens from the various localities could be recognised, except the Shan States individuals, which are more similar in part of the genital armature to the North Indian *anticrates*.

The chief distinction in the genital armature of *hermocrates* concerns the form of the dorsal lobe, which normally is shaped as in f. 78, and the form of the ventral ridge, which has the basal tooth (f. 74) less horizontal than it is in *anticrates*.

We have two individuals from Muong Gnow, Shan States, one darker than many Philippine Islands specimens, one intermediate in the development of the bands between *anticrates* and ordinary Philippine *hermocrates*. The dorsal lobe of the dark specimen (f. 76) is scarcely different from that of *anticrates*, being much broader than it normally is in *hermocrates* (compare f. 76 to 80); in the whiter individual, which in the wing-pattern is scarcely different from dark Sikkim examples of *anticrates*, the dorsal lobe is considerably narrower (f. 77).

The series of f. 76 to 80 represents the variation of the dorsal lobe. F. 78 is taken from a specimen from Kudat, North Borneo; the lobe is still narrower than in f. 77; the next two figures (79 and 80) represent the lobe of two Palawan individuals. The specimens from Kalao, Timor, Wetter, and Sumba have the lobes as in f. 78 to 80.

The *gradual* decrease in the size of the dorsal lobe from f. 75 (*anticrates*) to f. 76 (*hermocrates*), and from there to f. 80, is evident; and it is further obvious that the difference between the extreme form of the lobe of *hermocrates* (f. 80) and the lobe of *aristeus*, as well as the difference between the other extreme of *hermocrates* (f. 76) and *anticrates* (f. 75), amounts quantitatively to much less than the difference between the extremes of *hermocrates* (f. 76 and 80).

c. *P. aristeus aristeus* from the Southern and Northern Moluccas: f. 81 to 83.

The individuals from the various islands of the Moluccas, though individually variable, exhibit neither in the wing-pattern nor in the genital armature any character confined to one or the other of the islands, or group of islands. This subspecies is in pattern most nearly related to *hermocrates*, but is easily distinguished by the ground-colour of the underside being obviously darker.

The dorsal lobe of the valve (f. 81 and 82) is in all specimens examined slenderer than in *hermocrates*; the individual variation is slight. The ventral ridge the longest, most basal, tooth (right-hand side in figure) is nearly horizontal. The subdorsal process is simple, without denticulation.

There is no difference in the genital armature between the darker and the less dark specimens from Sikkim and Assam.

b. *P. aristeus hermocrates* from Burma to Timor, Borneo, Palawan, and the Philippine Islands; f. 74, 76 to 80.

We have examined individuals from the Shan States, Borneo, Palawan, the Philippine Islands, Sumba, Kalao, Wetter, and Timor. The individual variation in the pattern of the wings and in the size of the specimens is considerable, but we cannot find distinguishing characters which would necessitate a division of *hermocrates* into more subspecies; the Wetter and Timor individuals, from which islands we have only three altogether, are faintly different in the shape of the forewing, and may perhaps, on receipt of more material, be separable from *hermocrates*. An examination of the genital armature likewise did not furnish us with characters by which specimens from the various localities could be recognised, except the Shan States individuals, which are more similar in part of the genital armature to the North Indian *anticrates*.

The chief distinction in the genital armature of *hermocrates* concerns the form of the dorsal lobe, which normally is shaped as in f. 78, and the form of the ventral ridge, which has the basal tooth (f. 74) less horizontal than it is in *anticrates*.

We have two individuals from Muong Gnow, Shan States, one darker than many Philippine Islands specimens, one intermediate in the development of the bands between *anticrates* and ordinary Philippine *hermocrates*. The dorsal lobe of the dark specimen (f. 76) is scarcely different from that of *anticrates*, being much broader than it normally is in *hermocrates* (compare f. 76 to 80); in the whiter individual, which in the wing-pattern is scarcely different from dark Sikkim examples of *anticrates*, the dorsal lobe is considerably narrower (f. 77).

The series of f. 76 to 80 represents the variation of the dorsal lobe. F. 78 is taken from a specimen from Kudat, North Borneo; the lobe is still narrower than in f. 77; the next two figures (79 and 80) represent the lobe of two Palawan individuals. The specimens from Kalao, Timor, Wetter, and Sumba have the lobes as in f. 78 to 80.

The *gradual* decrease in the size of the dorsal lobe from f. 75 (*anticrates*) to f. 76 (*hermocrates*), and from there to f. 80, is evident; and it is further obvious that the difference between the extreme form of the lobe of *hermocrates* (f. 80) and the lobe of *aristeus*, as well as the difference between the other extreme of *hermocrates* (f. 76) and *anticrates* (f. 75), amounts quantitatively to much less than the difference between the extremes of *hermocrates* (f. 76 and 80).

c. *P. aristeus aristeus* from the Southern and Northern Moluccas: f. 81 to 83.

The individuals from the various islands of the Moluccas, though individually variable, exhibit neither in the wing-pattern nor in the genital armature any character confined to one or the other of the islands, or group of islands. This subspecies is in pattern most nearly related to *hermocrates*, but is easily distinguished by the ground-colour of the underside being obviously darker.

The dorsal lobe of the valve (f. 81 and 82) is in all specimens examined slenderer than in *hermocrates*; the individual variation is slight. The ventral ridge is much more extended than in the two preceding subspecies ; when seen from above, as in f. 82, it is a kind of half-ring ; f. 83 gives the same organ in a view from the dorsal side of the valve. The difference between the ridge of *aristeus* and that of *hermocrates* and *anticrates* is obvious enough without further comment. Intergradations in the form of the organ are unknown to us. F. 81 to 83 are taken from a Halmaheira individual.

The subdorsal process is denticulate, and is longer than in *hermocrates* and *anticrates*, projecting distinctly beyond the upper edge of the ventral lobe of the valve (f. 82).

d. *P. aristeus parmatus* from Queensland, New Guinea, and Waigeu.

This subspecies agrees externally so well with the Indian *P. aristeus anticrates* that Professor Eimer did not perceive the slight differences in colour and pattern which generally separate *parmatus* from *anticrates*, and which Mr. Rothschild pointed out on p. 419 of Vol. II. of this journal.

Although we know from several species that in forms which in the wing-colour and pattern are the most closely allied the genital armature is more different than in externally less closely allied forms, we were nevertheless much surprised to find that *aristeus parmatus* has, in opposition to *aristeus anticrates*, the same genital armature as *aristeus aristeus* ; we dare say exactly the same, as *we have not found a single character* by which the apparatus of *parmatus* could be distinguished from that of the Moluccan insect. This discovery is very important, as it shows evidently that, in order to understand the relation of a form, it is necessary to compare sets of entirely independent characters, and as it further proves that a form externally similar to another can be dissimilar in the genital armature, while it agrees in these organs with an externally very different form.

13. **Papilio rhesus** from Celebes, Saleyer, and Djampea; f. 84, 85.

Though Eimer removes this insect from *aristeus* and puts it into another group of species along with American species, such as *ajax*, all the characters by which *P. rhesus* is distinguished from *P. aristeus* are developments of the characters of *aristeus*. The only argument in favour of a relationship with *ajax* is the number of the black bands on the forewing ; in *rhesus* there is one band less than in *aristeus* ; but even this argument is not valid, as there very often occur specimens in which the usually absent band is indicated by a black spot, and as there are even examples in which this spot has developed to a distinct band. All the other characters of the wing-pattern speak against a relationship with *ajax*, and this statement is corroborated by the morphology of the *male* sexual armature and by the form of the eighth abdominal segment of the *female*. To begin with the latter, it will be sufficient to say that the eighth segment in *rhesus* is complete, as in *aristeus*, *agamemnon*, *sarpedon*, etc. (see f. 182, *sarpedon sarpedon* ; f. 185, *aristeus parmatus* ; f. 187, *macfarlanei*) ; whereas in *ajax* ♀ the eighth segment is incomplete, as in f. 181 (*podalirius*). The similarity in the armature of the valve of *rhesus* with that of *aristeus* will become evident by comparing f. 84 and 85 with 75 and 83.

The dorsal lobe of the valve of *rhesus* (f. 84) is much broader than even in the Indian *aristeus anticrates*, except the free apex, which is comparatively narrower: the subdorsal process is thin, and, as in *anticrates*, not dentate ; the ventral ridge is much more extended than in the two preceding subspecies ; when seen from above, as in f. 82, it is a kind of half-ring ; f. 83 gives the same organ in a view from the dorsal side of the valve. The difference between the ridge of *aristeus* and that of *hermocrates* and *anticrates* is obvious enough without further comment. Intergradations in the form of the organ are unknown to us. F. 81 to 83 are taken from a Halmaheira individual.

The subdorsal process is denticulate, and is longer than in *hermocrates* and *anticrates*, projecting distinctly beyond the upper edge of the ventral lobe of the valve (f. 82).

d. *P. aristeus parmatus* from Queensland, New Guinea, and Waigeu.

This subspecies agrees externally so well with the Indian *P. aristeus anticrates* that Professor Eimer did not perceive the slight differences in colour and pattern which generally separate *parmatus* from *anticrates*, and which Mr. Rothschild pointed out on p. 419 of Vol. II. of this journal.

Although we know from several species that in forms which in the wing-colour and pattern are the most closely allied the genital armature is more different than in externally less closely allied forms, we were nevertheless much surprised to find that *aristeus parmatus* has, in opposition to *aristeus anticrates*, the same genital armature as *aristeus aristeus* ; we dare say exactly the same, as *we have not found a single character* by which the apparatus of *parmatus* could be distinguished from that of the Moluccan insect. This discovery is very important, as it shows evidently that, in order to understand the relation of a form, it is necessary to compare sets of entirely independent characters, and as it further proves that a form externally similar to another can be dissimilar in the genital armature, while it agrees in these organs with an externally very different form.

13. **Papilio rhesus** from Celebes, Saleyer, and Djampea; f. 84, 85.

Though Eimer removes this insect from *aristeus* and puts it into another group of species along with American species, such as *ajax*, all the characters by which *P. rhesus* is distinguished from *P. aristeus* are developments of the characters of *aristeus*. The only argument in favour of a relationship with *ajax* is the number of the black bands on the forewing ; in *rhesus* there is one band less than in *aristeus* ; but even this argument is not valid, as there very often occur specimens in which the usually absent band is indicated by a black spot, and as there are even examples in which this spot has developed to a distinct band. All the other characters of the wing-pattern speak against a relationship with *ajax*, and this statement is corroborated by the morphology of the *male* sexual armature and by the form of the eighth abdominal segment of the *female*. To begin with the latter, it will be sufficient to say that the eighth segment in *rhesus* is complete, as in *aristeus*, *agamemnon*, *sarpedon*, etc. (see f. 182, *sarpedon sarpedon* ; f. 185, *aristeus parmatus* ; f. 187, *macfarlanei*) ; whereas in *ajax* ♀ the eighth segment is incomplete, as in f. 181 (*podalirius*). The similarity in the armature of the valve of *rhesus* with that of *aristeus* will become evident by comparing f. 84 and 85 with 75 and 83.

The dorsal lobe of the valve of *rhesus* (f. 84) is much broader than even in the Indian *aristeus anticrates*, except the free apex, which is comparatively narrower: the subdorsal process is thin, and, as in *anticrates*, not dentate ; the ventral ridge is almost shaped as in *aristeus aristeus* and *aristeus parmatus*, but the basi-dorsal portion of the half-ring is much higher than in these subspecies ; f. 84 gives a dorsal view of the ridge.

The affinities of *rhesus* are as follows : in the pattern of the wings it comes nearest to *hermocrates*, in the form of the dorsal lobe of the valve and the subdorsal process nearest to *anticrates* and *hermocrates*, in the form of the ventral ridge nearest to *aristeus* and *parmatus*.

The facts of variation illustrated by f. 72 to 85 are as follows:—

(1) *P. aristeus hermocrates* exhibits obvious variability in the shape of the dorsal lobe of the valve ; the extreme specimens come very near *anticrates* and *aristeus* respectively.

(2) That Shan States individual of *hermocrates* which is most "typical" in pattern has the dorsal lobe nearly identical with *anticrates*, while a specimen from the same locality which in pattern is almost identical with certain North Indian individuals of *anticrates* has the dorsal lobe much narrower.

(3) There are no intergradations between the form of the ventral ridge of *aristeus parmatus*, *aristeus aristeus*, and *rhesus* on one side, and *aristeus anticrates* and *aristeus hermocrates* on the other.

(4) The two Eastern subspecies, *parmatus* and *aristeus*, geographically the nearest related, are identical in the genital armature and conspicuously different in pattern.

(5) The two subspecies, *anticrates* and *parmatus*, inhabiting the extreme parts of the range are in pattern closely related, and in the genital armature very different.

14. **Papilio alcinous** from Japan, the Loo Choo Islands, Formosa, and China ; Nov. Zool. 1895. t. VI.

China is inhabited by several forms related to the Japanese *alcinous*, namely *confusus*, *impediens*, *plutonius*, and *mencius*. Of these we shall take here into consideration only the first, *confusus*, which differs externally in the ♂ from the Japanese Papilio in the body being more extended red, especially in the front of the head being clothed with red and with black hairs (while in the Japanese insect the head is all black), and in the submarginal spots of the hindwing being generally more brilliant red. The Formosa specimens agree with this Chinese form in colour, and so do the individuals from the Loo Choo Islands. The examination of the harpes of a long series of Chinese and Japanese individuals led to remarkable results which are laid down in Vol. II. of this journal. The results were as follows:—

The harpe of the black-headed Japanese insect is, in all specimens examined, very different from the harpe of the Chinese individuals, except in one individual which has the harpe like the Chinese specimens.

The red-headed Loo Choo specimens have the harpe like the black-headed Japanese specimens. We have here, therefore, a combination of the external characters of the Chinese form with the genital characters of the Japanese form.

Amongst the red-headed Chinese specimens one was found in which the harpe has the dentate ridge of the Japanese form and the free apical process of the normal Chinese form, and hence combines the characters of the harpe of the red-headed Chinese and black-headed Japanese Papilios.

is almost shaped as in *aristeus aristeus* and *aristeus parmatus*, but the basi-dorsal portion of the half-ring is much higher than in these subspecies ; f. 84 gives a dorsal view of the ridge.

The affinities of *rhesus* are as follows : in the pattern of the wings it comes nearest to *hermocrates*, in the form of the dorsal lobe of the valve and the subdorsal process nearest to *anticrates* and *hermocrates*. in the form of the ventral ridge nearest to *aristeus* and *parmatus*.

The facts of variation illustrated by f. 72 to 85 are as follows:—

(1) *P. aristeus hermocrates* exhibits obvious variability in the shape of the dorsal lobe of the valve ; the extreme specimens come very near *anticrates* and *aristeus* respectively.

(2) That Shan States individual of *hermocrates* which is most " typical " in pattern has the dorsal lobe nearly identical with *anticrates*, while a specimen from the same locality which in pattern is almost identical with certain North Indian individuals of *anticrates* has the dorsal lobe much narrower.

(3) There are no intergradations between the form of the ventral ridge of *aristeus parmatus*, *aristeus aristeus*, and *rhesus* on one side, and *aristeus anticrates* and *aristeus hermocrates* on the other.

(4) The two Eastern subspecies, *parmatus* and *aristeus*, geographically the nearest related, are identical in the genital armature and conspicuously different in pattern.

(5) The two subspecies, *anticrates* and *parmatus*, inhabiting the extreme parts of the range are in pattern closely related, and in the genital armature very different.

14. **Papilio alcinous** from Japan, the Loo Choo Islands, Formosa, and China ; Nov. Zool. 1895. t. VI.

China is inhabited by several forms related to the Japanese *alcinous*, namely *confusus*, *impediens*, *plutonius*, and *mencius*. Of these we shall take here into consideration only the first, *confusus*, which differs externally in the ♂ from the Japanese Papilio in the body being more extended red. especially in the front of the head being clothed with red and with black hairs (while in the Japanese insect the head is all black), and in the submarginal spots of the hindwing being generally more brilliant red. The Formosa specimens agree with this Chinese form in colour, and so do the individuals from the Loo Choo Islands. The examination of the harpes of a long series of Chinese and Japanese individuals led to remarkable results which are laid down in Vol. II. of this journal. The results were as follows:—

The harpe of the black-headed Japanese insect is, in all specimens examined. very different from the harpe of the Chinese individuals, except in one individual which has the harpe like the Chinese specimens.

The red-headed Loo Choo specimens have the harpe like the black-headed Japanese specimens. We have here, therefore, a combination of the external characters of the Chinese form with the genital characters of the Japanese form.

Amongst the red-headed Chinese specimens one was found in which the harpe has the dentate ridge of the Japanese form and the free apical process of the normal Chinese form, and hence combines the characters of the harpe of the red-headed Chinese and black-headed Japanese Papilios.

The facts are briefly as follows :—

(1) Japan : Head black. Harpe with dentate ridge, without free apical process : one specimen like (3).

(2) Loo Choo Islands : Head as in (3). Harpe as in (1).

(3) China and Formosa : Head red. Harpe without dentate ridge, with free apical process ; one specimen with dentate ridge (= 1) and with free apical process (= 3).

The only inference from these facts logically possible is that neither the red colour of part of the hairs of the head, nor the form of the harpe, is in the Papilios in question of specific value. The present case reminds one strongly of that of *P. sarpedon* as explained on p. 478.

15. **Papilio aristolochiae**; f. 86 to 95.

The group of Papilios to which the present species belongs has the valve much reduced ; the harpe does not vary to any extent, while the *uncus* (dorsal part of the tenth segment, according to Peytoureau) is very variable. To show the amount of variation in one of the species, we figure the uncus of three Sikkim individuals of *P. aristolochiae aristolochiae* (f. 86 to 88), of three Sambawa specimens of *P. aristolochiae austrosundanus* (f. 89 to 91), and of four Bunguran examples of *P. aristolochiae antiphus* (f. 92 to 95). The variability of the uncus within each subspecies of *aristolochiae* is so great that we fail to perceive any character in that organ which could serve to distinguish the three (in external features easily recognisable) subspecies by.

B. Female Genital Armature.

Peytoureau,* in his researches on the morphology of the last segments of the abdomen of the *female Lepidoptera*, comes to the conclusion that there are, as in the *male*, ten segments, the anal segment of the *female* imago, consisting of two lateral pieces comparable in form to the valves of the *male* and having the function of a protector of the anus and the orifice of the oviduct, being homologous to the ninth and tenth segments of the pupa and larva ; the orifice of the oviduct has the same position as the penis underneath the anus between the ninth and tenth segments. The variation of the anal segment is of no importance for our present purposes. The orifice of the vagina is separated from the orifice of the oviduct, and is situated between the seventh and the eighth segments ; in consequence of the development of the copulatory apparatus the eighth, not the seventh, segment has undergone great changes. The form of the segment, as well as of the vaginal armature, is in a live specimen easily perceivable when one gently presses the abdomen ; in a dried-up individual the apparatus is concealed, being entirely removed into the vaginal cavity, the opening of which is closed by the seventh and eighth segments being in contact. As it was, in the first place, not the aim of our researches to find characters in the morphology of the abdomen by which the higher divisions in the system of *Lepidoptera*, such as families and subfamilies, could be distinguished, but to try whether the morphological characters of the last segments could be made use of in diagnostic work relating to the lower degrees of division, genera and species, and particularly whether within the limits of a species there was in the copulatory apparatus a variation similar in kind and extent to that of the *male* organs of copulation, it was necessary to study the organs in question *in situ*, in order to be able to

---

* See note, p. 461.

The facts are briefly as follows :—

(1) Japan : Head black. Harpe with dentate ridge, without free apical process : one specimen like (3).

(2) Loo Choo Islands : Head as in (3). Harpe as in (1).

(3) China and Formosa : Head red. Harpe without dentate ridge, with free apical process ; one specimen with dentate ridge (= 1) and with free apical process (= 3).

The only inference from these facts logically possible is that neither the red colour of part of the hairs of the head, nor the form of the harpe, is in the Papilios in question of specific value. The present case reminds one strongly of that of *P. sarpedon* as explained on p. 478.

15. **Papilio aristolochiae**; f. 86 to 95.

The group of Papilios to which the present species belongs has the valve much reduced ; the harpe does not vary to any extent, while the *uncus* (dorsal part of the tenth segment, according to Peytoureau) is very variable. To show the amount of variation in one of the species, we figure the uncus of three Sikkim individuals of *P. aristolochiae aristolochiae* (f. 86 to 88), of three Sambawa specimens of *P. aristolochiae austrosundanus* (f. 89 to 91), and of four Bunguran examples of *P. aristolochiae antiphus* (f. 92 to 95). The variability of the uncus within each subspecies of *aristolochiae* is so great that we fail to perceive any character in that organ which could serve to distinguish the three (in external features easily recognisable) subspecies by.

B. FEMALE GENITAL ARMATURE.

Peytoureau,* in his researches on the morphology of the last segments of the abdomen of the *female Lepidoptera*, comes to the conclusion that there are, as in the *male*, ten segments, the anal segment of the *female* imago, consisting of two lateral pieces comparable in form to the valves of the *male* and having the function of a protector of the anus and the orifice of the oviduct, being homologous to the ninth and tenth segments of the pupa and larva ; the orifice of the oviduct has the same position as the penis underneath the anus between the ninth and tenth segments. The variation of the anal segment is of no importance for our present purposes. The orifice of the vagina is separated from the orifice of the oviduct, and is situated between the seventh and the eighth segments; in consequence of the development of the copulatory apparatus the eighth, not the seventh, segment has undergone great changes. The form of the segment, as well as of the vaginal armature, is in a live specimen easily perceivable when one gently presses the abdomen ; in a dried-up individual the apparatus is concealed, being entirely removed into the vaginal cavity, the opening of which is closed by the seventh and eighth segments being in contact. As it was, in the first place, not the aim of our researches to find characters in the morphology of the abdomen by which the higher divisions in the system of *Lepidoptera*, such as families and subfamilies, could be distinguished, but to try whether the morphological characters of the last segments could be made use of in diagnostic work relating to the lower degrees of division, genera and species, and particularly whether within the limits of a species there was in the copulatory apparatus a variation similar in kind and extent to that of the *male* organs of copulation, it was necessary to study the organs in question *in situ*, in order to be able to

---

* See note, p. 461.

compare the position and direction and the outline of the homologous parts of the apparatus of the allied insects, and thus to be able to observe minute differences in the most nearly related forms. As in live specimens, or in individuals shortly after death, a pressure of the abdomen sufficed to bring the organs in question fully in view, it was evident that a method of preparation of dried specimens would be successful, if the intersegmental membranes of the end of the abdomen were so relaxed that the whole apparatus could be pushed out without destroying the connection between the several organs. The method of preparation we employ is quite sufficient for our purpose, and has the great advantage of being very simple. We cut off the last four segments, soak them in hot alcohol and water, remove the eggs, scales, etc., with the help of a pin and brush, press the segments gently, and leave the abdomen in alcohol and water until the segments are freely moveable ; then we press the head of a pin from the inside of the abdomen against the vaginal bulb, and push it gently out, taking care that the membranes do not get torn. The eggs and the *bursa copulatrix* ought to be preserved.

While in a live specimen the membraneous and the more chitinised parts in the vaginal region are easily distinguished by their colour, in a dry individual all the parts are more or less brown, and, though the strongly chitinised organs are recognisable by their gloss, the exact limits between the membrane and the chitinised pieces which it connects are often obscured.

According to the development of the eighth segment the Eastern Papilios can be divided into two groups—such in which the eighth segment forms a complete ring without longitudinal sutures (f. 182), and such in which the ventral plate is absent. To the first group belong nearly all those Indian and African species examined in which the first subcostal nervule of the forewing anastomoses with the costa, except *P. mandarinus* and allies, and to the second group all the other Papilios examined, inclusive of *Troides* = *Ornithoptera*. The combination of an obvious character in neuration with a still more conspicuous particularity in the development of the eighth abdominal segment of the *females* of the species allied to *agamemnon*, *sarpedon*, *codrus*, *aristeus*, and *antiphates* of the Indo-Australian Region, and of *antheus*, *leonidas*, *pylades*, etc., from Africa, indicates certainly more than mere similarity in form.

The special copulatory apparatus consists of processes, ridges, tubercles, and folds near the vaginal orifice, all more or less chitinised, often dentate and hook-shaped. It is not a modification of the ventral plate of the eighth segment, but is an independent structure of the intersegmental membrane. The variety of the apparatus in the various species is startling, as a glance at f. 156 to 182 will show. The orifice of the vagina, marked *e* in the figures on Pl. XIX., has in the diverse groups of *Papilio* a different position : in *P. alcinous*, *philoxenus*, and allies, it has a ventral (*recte* basal or anterior) (f. 179), in *podalirius* and allies (f. 181) a more dorsal (*recte* apical or posterior) position.

The variability of the copulatory apparatus we explain by figures only of four species ; this must suffice for the present. But to demonstrate the classificatory value of the armature we give figures of seven more species.

16. **Papilio machaon**; f. 156 to 159.

The figures are taken from a British individual. When examining the intersegmental membrane which bears the orifice of the vagina and the chitinised prehensile apparatus we perceive (f. 157) a somewhat lyriform or horseshoe-shaped compare the position and direction and the outline of the homologous parts of the apparatus of the allied insects, and thus to be able to observe minute differences in the most nearly related forms. As in live specimens, or in individuals shortly after death, a pressure of the abdomen sufficed to bring the organs in question fully in view, it was evident that a method of preparation of dried specimens would be successful, if the intersegmental membranes of the end of the abdomen were so relaxed that the whole apparatus could be pushed out without destroying the connection between the several organs. The method of preparation we employ is quite sufficient for our purpose, and has the great advantage of being very simple. We cut off the last four segments, soak them in hot alcohol and water, remove the eggs, scales, etc., with the help of a pin and brush, press the segments gently, and leave the abdomen in alcohol and water until the segments are freely moveable; then we press the head of a pin from the inside of the abdomen against the vaginal bulb, and push it gently out, taking care that the membranes do not get torn. The eggs and the *bursa copulatrix* ought to be preserved.

While in a live specimen the membraneous and the more chitinised parts in the vaginal region are easily distinguished by their colour, in a dry individual all the parts are more or less brown, and, though the strongly chitinised organs are recognisable by their gloss, the exact limits between the membrane and the chitinised pieces which it connects are often obscured.

According to the development of the eighth segment the Eastern Papilios can be divided into two groups—such in which the eighth segment forms a complete ring without longitudinal sutures (f. 182), and such in which the ventral plate is absent. To the first group belong nearly all those Indian and African species examined in which the first subcostal nervule of the forewing anastomoses with the costa, except *P. mandarinus* and allies, and to the second group all the other Papilios examined, inclusive of *Troides* = *Ornithoptera*. The combination of an obvious character in neuration with a still more conspicuous particularity in the development of the eighth abdominal segment of the *females* of the species allied to *agamemnon*, *sarpedon*, *codrus*, *aristeus*, and *antiphates* of the Indo-Australian Region, and of *antheus*, *leonidas*, *pylades*, etc., from Africa, indicates certainly more than mere similarity in form.

The special copulatory apparatus consists of processes, ridges, tubercles, and folds near the vaginal orifice, all more or less chitinised, often dentate and hook-shaped. It is not a modification of the ventral plate of the eighth segment, but is an independent structure of the intersegmental membrane. The variety of the apparatus in the various species is startling, as a glance at f. 156 to 182 will show. The orifice of the vagina, marked *e* in the figures on Pl. XIX., has in the diverse groups of *Papilio* a different position: in *P. alcinous*, *philoxenus*, and allies, it has a ventral (*recte* basal or anterior) (f. 179), in *podalirius* and allies (f. 181) a more dorsal (*recte* apical or posterior) position.

The variability of the copulatory apparatus we explain by figures only of four species; this must suffice for the present. But to demonstrate the classificatory value of the armature we give figures of seven more species.

16. **Papilio machaon**; f. 156 to 159.

The figures are taken from a British individual. When examining the intersegmental membrane which bears the orifice of the vagina and the chitinised prehensile apparatus we perceive (f. 157) a somewhat lyriform or horseshoe-shaped buckle (*b*), which is a chitinised portion of the membrane itself, and does not protrude free; its ventral and lateral edges form a slightly raised ridge, as can be seen in f. 156. The ventral part of this buckle is produced into two processes (*a*), which are thin in a dorso-ventral sense, but divided longitudinally into a left and a right half, which stand at a blunt angle to one another in consequence of the middle line of the process being more dorsal than the lateral edges. At the base each process is constricted (f. 158), while the edge of the apical half is armed with teeth. In a side view the process (f. 156 and 159) appears plainly as a dilatation of the buckle *b*. The vagina *v* (f. 159) is behind the middle of the median piece of the buckle, and marked in f. 157 behind the two processes as a black spot.

The series of *females* examined has not been very great, and hence we do not yet know whether there is not some variation in the form of the armature in the various subspecies. From what we have seen we must conclude that if there is such a variation it must be very slight, as neither the European and Asiatic nor some American forms of *P. machaon* presented any obvious deviation from what we have figured on Pl. XIX. And this would be entirely in accordance with what we have found in the *male* genital armature of *machaon*, as far as a distinction between the genital armature of the various subspecies of this species goes. We can safely say that in *P. machaon* from Europe and Asia—

(1) There is no character in the genital armature of both sexes of any of the subspecies by which the greater percentage of the individuals could be distinguished:

(2) There are obvious characters in the colour and pattern of the wing and body of each subspecies by which the greater percentage of the individuals, but not every specimen, can be distinguished.

The genital armature of *P. xuthus* is entirely different from that of *machaon*.*

17. **Papilio polytes**; f. 160 and 161.

The *female* of this species is polymorphic; we have examined the three *female* forms from Ceylon and North India, the two forms from Borneo, the three from the Philippine Islands, and also a single specimen of each of the subspecies from Celebes, Sangir, Sulla Islands, Amboina, and Halmaheira.

There is a good deal of individual variation in the apparatus of *P. polytes*, but this variation is entirely independent of the colour and pattern of the wings, and hence the various forms of the *female* of each subspecies must be pronounced to be identical in the genital armature; ♀-f. *romulus*, ♀-f. *cyrus*, and ♀-f. *polytes* do not present any character in the vaginal armature by which one form is distinguished from the other, and so it is with ♀-f. *theseus* and ♀-f. *civilis*, and so on.

The intersegmental membrane (f. 160) is just underneath the eighth segment at each side thickened and corrugated, the corrugated portion having an elongate-ovate outline; round the orifice of the vagina there is a low ridge continued upwards to the hinder end of the corrugate mark; this ridge is raised into five processes, one ventral and two on each side lateral. The form of the processes is visible in f. 161, which represents the apparatus flattened out and viewed from the anal side: the ventral process is rounded, the lateral ones are sharply pointed, the lower one is the longest. The length of the lateral processes is variable. Above the vagina there is a rounded tubercle, *t*, present in all allies.

---

* This confirms Dr. Seitz's opinion that *xuthus* is not a very near relation of *machaon*. See *Soc. Ent.*, 1895, p. 130.

buckle (*b*), which is a chitinised portion of the membrane itself, and does not protrude free; its ventral and lateral edges form a slightly raised ridge, as can be seen in f. 156. The ventral part of this buckle is produced into two processes (*a*), which are thin in a dorso-ventral sense, but divided longitudinally into a left and a right half, which stand at a blunt angle to one another in consequence of the middle line of the process being more dorsal than the lateral edges. At the base each process is constricted (f. 158), while the edge of the apical half is armed with teeth. In a side view the process (f. 156 and 159) appears plainly as a dilatation of the buckle *b*. The vagina *v* (f. 159) is behind the middle of the median piece of the buckle, and marked in f. 157 behind the two processes as a black spot.

The series of *females* examined has not been very great, and hence we do not yet know whether there is not some variation in the form of the armature in the various subspecies. From what we have seen we must conclude that if there is such a variation it must be very slight, as neither the European and Asiatic nor some American forms of *P. machaon* presented any obvious deviation from what we have figured on Pl. XIX. And this would be entirely in accordance with what we have found in the *male* genital armature of *machaon*, as far as a distinction between the genital armature of the various subspecies of this species goes. We can safely say that in *P. machaon* from Europe and Asia—

(1) There is no character in the genital armature of both sexes of any of the subspecies by which the greater percentage of the individuals could be distinguished:

(2) There are obvious characters in the colour and pattern of the wing and body of each subspecies by which the greater percentage of the individuals, but not every specimen, can be distinguished.

The genital armature of *P. xuthus* is entirely different from that of *machaon*.*

17. **Papilio polytes**; f. 160 and 161.

The *female* of this species is polymorphic; we have examined the three *female* forms from Ceylon and North India, the two forms from Borneo, the three from the Philippine Islands, and also a single specimen of each of the subspecies from Celebes, Sangir, Sulla Islands, Amboina, and Halmaheira.

There is a good deal of individual variation in the apparatus of *P. polytes*, but this variation is entirely independent of the colour and pattern of the wings, and hence the various forms of the *female* of each subspecies must be pronounced to be identical in the genital armature; ♀-f. *romulus*, ♀-f. *cyrus*, and ♀-f. *polytes* do not present any character in the vaginal armature by which one form is distinguished from the other, and so it is with ♀-f. *theseus* and ♀-f. *civilis*, and so on.

The intersegmental membrane (f. 160) is just underneath the eighth segment at each side thickened and corrugated, the corrugated portion having an elongate-ovate outline; round the orifice of the vagina there is a low ridge continued upwards to the hinder end of the corrugate mark; this ridge is raised into five processes, one ventral and two on each side lateral. The form of the processes is visible in f. 161, which represents the apparatus flattened out and viewed from the anal side: the ventral process is rounded, the lateral ones are sharply pointed, the lower one is the longest. The length of the lateral processes is variable. Above the vagina there is a rounded tubercle, *t*, present in all allies.

---

* This confirms Dr. Seitz's opinion that *xuthus* is not a very near relation of *machaon*. See *Soc. Ent.*, 1895, p. 130.

The various subspecies do not exhibit any obvious difference in the form of the ridge, except perhaps the forms from the Moluccas. We have examined only one individual of the two subspecies from Amboina and Halmaheira. These individuals showed some difference in the length of the lateral teeth ; but as in the Indian, Bornean, and Philippine insects, of which we have examined several specimens, the teeth vary according to the individual specimens, the difference in the Halmaheira and Amboina examples can just as well be due to individual as to subspecific variation. In the *male* sex we have found that the various subspecies are in the genital armature connected by intergradations, but that nearly all the specimens of each subspecies are pretty well recognisable by the form of the harpe. In the *female* sex the difference in the vaginal armature, if present, is certainly much fainter; but we shall see later on that the difference corresponding to that in the harpes does not exist in the chitinised processes, but in the folding of the membrane. and is, when slight, not perceivable in consequence of the shrivelling of the membrane in the dry specimens.

18. **Papilio ambrax** : f. 162.

Though in pattern the *female* of this species comes very near that of *P. polytes nicanor*, so near indeed that entomologists like Kirsch and Snellen have mistaken it for *polytes*, there is a constant and very conspicuous difference in the vaginal armature of the two species. F. 162 represents the apparatus of a specimen from New Guinea ; the ventral process *a* of f. 161 is here wanting, and this character we have found to be constant in all the twenty odd *females* of *ambrax* examined. Besides, the lower lateral tooth is generally somewhat shorter than in *polytes*. The variability of the ridge is similar to that of *polytes*. The Queenslandian subspecies does not, to our knowledge, present any distinguishing character from the New Guinean subspecies in the form of the ridge.

The representative species from the Bismarck Archipelago and the Solomon Islands we have not yet examined.

19. **Papilio aegeus** ; f. 163 to 169, 176.

The individual variability of the vaginal armature is in this species very great, while an examination of a longer series of specimens from New Guinea (*aegeus ormenus*) and Queensland (*aegeus aegeus*) proved that the variation according to locality is very slight. The vagina is surrounded by three high processes which are dilatations of a high ridge. The position and general form of the armature is represented by the half-diagrammatic figure 165. The ventral process is the largest, and is narrowed from the middle towards the base and the apex ; the apical half is dentate, divided by a median sinus into two lobes of variable length (f. 166 and 167), and is curved dorsally (f. 163); ventrally the ridge is, like the processes of *P. machaon*, longitudinally concave, and is provided with a rounded middle keel (f. 164, *m*) which does not reach the apex. The lateral process *b* is seldom simple in outline; mostly it is more or less strongly dentate (f. 166). Above the orifice of the vagina *v* there stands the supravaginal tubercle *t*. The intersegmental membrane is, moreover, raised into a vertical fold *f* (f. 163 and 164). which stands in connection with the vaginal ridge.

a. *P. aegeus ormenus*: f. 165 to 166, 176.

The *female* of this subspecies is polymorphic. As in the case of *P. polytes*, we have found no characters in the genital armature peculiar to one or the other of

The various subspecies do not exhibit any obvious difference in the form of the ridge, except perhaps the forms from the Moluccas. We have examined only one individual of the two subspecies from Amboina and Halmaheira. These individuals showed some difference in the length of the lateral teeth ; but as in the Indian, Bornean, and Philippine insects, of which we have examined several specimens, the teeth vary according to the individual specimens, the difference in the Halmaheira and Amboina examples can just as well be due to individual as to subspecific variation. In the *male* sex we have found that the various subspecies are in the genital armature connected by intergradations, but that nearly all the specimens of each subspecies are pretty well recognisable by the form of the harpe. In the *female* sex the difference in the vaginal armature, if present, is certainly much fainter; but we shall see later on that the difference corresponding to that in the harpes does not exist in the chitinised processes, but in the folding of the membrane, and is, when slight, not perceivable in consequence of the shrivelling of the membrane in the dry specimens.

18. **Papilio ambrax** : f. 162.

Though in pattern the *female* of this species comes very near that of *P. polytes nicanor*, so near indeed that entomologists like Kirsch and Snellen have mistaken it for *polytes*, there is a constant and very conspicuous difference in the vaginal armature of the two species. F. 162 represents the apparatus of a specimen from New Guinea ; the ventral process *a* of f. 161 is here wanting, and this character we have found to be constant in all the twenty odd *females* of *ambrax* examined. Besides, the lower lateral tooth is generally somewhat shorter than in *polytes*. The variability of the ridge is similar to that of *polytes*. The Queenslandian subspecies does not, to our knowledge, present any distinguishing character from the New Guinean subspecies in the form of the ridge.

The representative species from the Bismarck Archipelago and the Solomon Islands we have not yet examined.

19. **Papilio aegeus** ; f. 163 to 169, 176.

The individual variability of the vaginal armature is in this species very great, while an examination of a longer series of specimens from New Guinea (*aegeus ormenus*) and Queensland (*aegeus aegeus*) proved that the variation according to locality is very slight. The vagina is surrounded by three high processes which are dilatations of a high ridge. The position and general form of the armature is represented by the half-diagrammatic figure 165. The ventral process is the largest, and is narrowed from the middle towards the base and the apex ; the apical half is dentate, divided by a median sinus into two lobes of variable length (f. 166 and 167), and is curved dorsally (f. 163); ventrally the ridge is, like the processes of *P. machaon*, longitudinally concave, and is provided with a rounded middle keel (f. 164, *m*) which does not reach the apex. The lateral process *b* is seldom simple in outline; mostly it is more or less strongly dentate (f. 166). Above the orifice of the vagina *c* there stands the supravaginal tubercle *t*. The intersegmental membrane is, moreover, raised into a vertical fold *f* (f. 163 and 164), which stands in connection with the vaginal ridge.

a. *P. aegeus ormenus*: f. 163 to 166, 176.

The *female* of this subspecies is polymorphic. As in the case of *P. polytes*, we have found no characters in the genital armature peculiar to one or the other of the *female* forms. The specimens figured are from near Dorey, Dutch New Guinea. In f. 166 the left lateral ridge is not drawn; the ventral process of this specimen is at the apex much deeper sinuate than that of f. 164, and the lateral process is much broader and multidentate, while the process is not dentate in f. 163 and 164. The anal segment and the supravaginal tubercle *t* is represented by f. 176.

b. *P. aegeus aegeus*: f. 167 to 169.

The *female* of this subspecies is monomorphic in colour and pattern. The variability of the vaginal armature is illustrated by f. 167 to 169. The ventral process is slenderer at the base than in *aegeus ormenus*, and the lateral process has mostly on the outer side a slightly raised carina (f. 168 and 169). In f. 167 the teeth of the lateral and ventral processes, and in f. 169 those of the lateral process, are mostly obliterated; the dentition of the lateral process represented in f. 168 is restricted to the upper edge.

20. Papilio rumanzovius; f. 170 and 178.

There are four series of species of Papilios which are closely allied to one another, the groups of *P. memnon*, *P. aegeus*, *P. deiphobus*, and *P. lampsacus*. We represent for comparison the *female* sexual armature of a species of the first three groups; the close relationship of the insects in question finds an expression in the similarity of the genital armature of *male* and *female*.

F. 170 is taken from a specimen of *P. rumanzovius* ♀-f. *rumanzovius*. The ventral process is broadest towards the base, its apex is irregularly truncate, the dentition of the process of *aegeus* (f. 166 to 169) is absent; the median keel on the ventral side of the process of *aegeus* is here separated into a number of irregular, longitudinal, slightly raised folds and wrinkles. The lateral process is less high and leans over dorsally. The supravaginal tubercle, which in *aegeus* (f. 176) is small, and near which the membrane is inobviously folded, is in *rumanzovius* large (f. 178), and the membrane between it and the anal segment (ix. + x.) is regularly and heavily folded transversely, the folds being limited laterally by a longitudinal fold.

21. Papilio memnon; f. 171 to 175, 177.

Like *P. polytes* and *P. aegeus ormenus*, this species has a polymorphic *female* in most localities; we have examined a number of tailed and tailless individuals from North India, Java, Nias, and Borneo, and come to the same conclusions as in the case of the two before-mentioned Papilios, that the subspecies are extremely slightly different in the *female* genital armature, and that the various forms of the *female* of each subspecies do not exhibit any characters in the vaginal apparatus peculiar to one or the other of the forms. The individual variability is as great, or even greater, than in *ormenus*.

The chief features by which the vaginal armature of *memnon* can be distinguished from that of *aegeus*, to which it comes rather near, are as follows: the ventral process is broader basally, and the median keel of the underside (ventral side) is widened out laterally into two ridges which rise under a small angle from the plane of the main process (f. 173, *m*). The lateral process (*b*) is higher than in *P. aegeus*, and divides very often at its dorsal edge in an outer (f. 174 and the *female* forms. The specimens figured are from near Dorey, Dutch New Guinea. In f. 166 the left lateral ridge is not drawn; the ventral process of this specimen is at the apex much deeper sinuate than that of f. 164, and the lateral process is much broader and multidentate, while the process is not dentate in f. 163 and 164. The anal segment and the supravaginal tubercle *t* is represented by f. 176.

b. *P. aegeus aegeus* : f. 167 to 169.

The *female* of this subspecies is monomorphic in colour and pattern. The variability of the vaginal armature is illustrated by f. 167 to 169. The ventral process is slenderer at the base than in *aegeus ormenus*, and the lateral process has mostly on the outer side a slightly raised carina (f. 168 and 169). In f. 167 the teeth of the lateral and ventral processes, and in f. 169 those of the lateral process, are mostly obliterated; the dentition of the lateral process represented in f. 168 is restricted to the upper edge.

20. **Papilio rumanzovius** ; f. 170 and 178.

There are four series of species of Papilios which are closely allied to one another, the groups of *P. memnon*, *P. aegeus*, *P. deiphobus*, and *P. lampsacus*. We represent for comparison the *female* sexual armature of a species of the first three groups; the close relationship of the insects in question finds an expression in the similarity of the genital armature of *male* and *female*.

F. 170 is taken from a specimen of *P. rumanzovius* ♀-f. *rumanzovius*. The ventral process is broadest towards the base, its apex is irregularly truncate, the dentition of the process of *aegeus* (f. 166 to 169) is absent; the median keel on the ventral side of the process of *aegeus* is here separated into a number of irregular, longitudinal, slightly raised folds and wrinkles. The lateral process is less high and leans over dorsally. The supravaginal tubercle, which in *aegeus* (f. 176) is small, and near which the membrane is inobviously folded, is in *rumanzovius* large (f. 178), and the membrane between it and the anal segment (ix. + x.) is regularly and heavily folded transversely, the folds being limited laterally by a longitudinal fold.

21. **Papilio memnon**; f. 171 to 175, 177.

Like *P. polytes* and *P. aegeus ormenus*, this species has a polymorphic *female* in most localities; we have examined a number of tailed and tailless individuals from North India, Java, Nias, and Borneo, and come to the same conclusions as in the case of the two before-mentioned Papilios, that the subspecies are extremely slightly different in the *female* genital armature, and that the various forms of the *female* of each subspecies do not exhibit any characters in the vaginal apparatus peculiar to one or the other of the forms. The individual variability is as great, or even greater, than in *ormenus*.

The chief features by which the vaginal armature of *memnon* can be distinguished from that of *aegeus*, to which it comes rather near, are as follows: the ventral process is broader basally, and the median keel of the underside (ventral side) is widened out laterally into two ridges which rise under a small angle from the plane of the main process (f. 173, *m*). The lateral process (*b*) is higher than in *P. aegeus*, and divides very often at its dorsal edge in an outer (f. 174 and

175, *o*) and inner ridge (*a*). The outline of the ventral and lateral ridges is very variable, as f. 172 to 175 show.

The supravaginal tubercle and the anal segment are represented in f. 177; the tubercle is similar to that of *P. aegeus*, but it is surrounded by two rather heavy folds which in *aegeus* are scarcely marked.

22. **Papilio alcinous**; f. 179 and 180.

The vaginal orifice is more ventral than in the preceding species, and the armature is very simple. Just above the vagina the membrane is smooth and more strongly chitinised, and bears a roundish impression (f. 179, *i*). From the lower edge of the eighth segment downwards extends a broad fold, *f*, which is also more chitinised than the rest of the intersegmental membrane, especially at two points where the fold has a bulbose appearance.

We have examined but two individuals each of the Chinese *P. alcinous confusus* and the Japanese *P. alcinous alcinous*, and find some obvious distinguishing characters between the two subspecies. In the Chinese form (f. 180) the membrane underneath the orifice of the vagina is strongly folded longitudinally, in the Japanese insect the membrane is smooth there; the supravaginal impression *i* is in *confusus* small, in *alcinous* large; the lateral fold is in *confusus* extended down to the ventral side as a conspicuously raised fold, while in *alcinous* the ventral portion of the fold is only slightly raised. A specimen from the Loo Choo Islands we unfortunately could not compare.

In the so-called nauseous species of *Papilio* allied to *alcinous*, *philoxenus*, and *aristolochiae* the vaginal armature is as a rule very simple.

23. **Papilio podalirius**; f. 181.

We figure the end of the abdomen of this European species for two reasons: first, because it enables the reader who is not acquainted with the exotic Papilios to compare the two common European species; and secondly, because the form of the eighth segment is entirely different from that of the Asiatic *P. antiphates*, *aristeus*, etc., which bear a superficial resemblance in pattern to *P. podalirius*.

The vaginal orifice is more dorsal, or rather apical, than in the preceding and following species here dealt with; the membrane round the orifice is strongly chitinised, forming a round plate-like organ, the edge of which is raised; the middle portion of the organ gradually raises and is highest just underneath the vaginal orifice; near the ventral edge of the eighth segment the edge of the discus-like organ fuses together with a strong oblique fold which is parallel to the ventral margin of that segment. The latter itself is incomplete, there being no ventral plate to it, but the posterior lateral angles almost meet above the vagina; the segment thus stands in development intermediate between the preceding species and the species here following. In the American allies of *P. podalirius* (*P. ajax*, etc.) the eighth segment is as in *podalirius* (or nearly so), and not as in *antiphates* and *aristeus*, which have it as in f. 182 (or nearly so). In *P. leosthenes* from Australia the segment agrees on the whole also with that of *podalirius*, and has also in *P. mandarinus* no ventral plate. Hence, in the development of the eighth abdominal segment *podalirius*, *leosthenes*, *ajax*, would be more nearly related to one another than to *aristeus*, *antheus*, etc., a statement which stands in direct opposition to the kind of relation at which Professor Eimer arrives by his interpretation of the wing-pattern; while, on the other hand, the absence of a ventral

175, *o*) and inner ridge (*u*). The outline of the ventral and lateral ridges is very variable, as f. 172 to 175 show.

The supravaginal tubercle and the anal segment are represented in f. 177; the tubercle is similar to that of *P. aegeus*, but it is surrounded by two rather heavy folds which in *aegeus* are scarcely marked.

22. **Papilio alcinous**; f. 179 and 180.

The vaginal orifice is more ventral than in the preceding species, and the armature is very simple. Just above the vagina the membrane is smooth and more strongly chitinised, and bears a roundish impression (f. 179, *i*). From the lower edge of the eighth segment downwards extends a broad fold, *f*, which is also more chitinised than the rest of the intersegmental membrane, especially at two points where the fold has a bulbose appearance.

We have examined but two individuals each of the Chinese *P. alcinous confusus* and the Japanese *P. alcinous alcinous*, and find some obvious distinguishing characters between the two subspecies. In the Chinese form (f. 180) the membrane underneath the orifice of the vagina is strongly folded longitudinally, in the Japanese insect the membrane is smooth there; the supravaginal impression *i* is in *confusus* small, in *alcinous* large; the lateral fold is in *confusus* extended down to the ventral side as a conspicuously raised fold, while in *alcinous* the ventral portion of the fold is only slightly raised. A specimen from the Loo Choo Islands we unfortunately could not compare.

In the so-called nauseous species of *Papilio* allied to *alcinous*, *philoxenus*, and *aristolochiae* the vaginal armature is as a rule very simple.

23. **Papilio podalirius**; f. 181.

We figure the end of the abdomen of this European species for two reasons: first, because it enables the reader who is not acquainted with the exotic Papilios to compare the two common European species; and secondly, because the form of the eighth segment is entirely different from that of the Asiatic *P. antiphates*, *aristeus*, etc., which bear a superficial resemblance in pattern to *P. podalirius*.

The vaginal orifice is more dorsal, or rather apical, than in the preceding and following species here dealt with; the membrane round the orifice is strongly chitinised, forming a round plate-like organ, the edge of which is raised; the middle portion of the organ gradually raises and is highest just underneath the vaginal orifice; near the ventral edge of the eighth segment the edge of the discus-like organ fuses together with a strong oblique fold which is parallel to the ventral margin of that segment. The latter itself is incomplete, there being no ventral plate to it, but the posterior lateral angles almost meet above the vagina; the segment thus stands in development intermediate between the preceding species and the species here following. In the American allies of *P. podalirius* (*P. ajax*, etc.) the eighth segment is as in *podalirius* (or nearly so), and not as in *antiphates* and *aristeus*, which have it as in f. 182 (or nearly so). In *P. leosthenes* from Australia the segment agrees on the whole also with that of *podalirius*, and has also in *P. mandarinus* no ventral plate. Hence, in the development of the eighth abdominal segment *podalirius*, *leosthenes*, *ajax*, would be more nearly related to one another than to *aristeus*, *antheus*, etc., a statement which stands in direct opposition to the kind of relation at which Professor Eimer arrives by his interpretation of the wing-pattern; while, on the other hand, the absence of a ventral connection of the lateral plates of the summit in *podalirius*, *mandarinus*, *ajax*, *leosthenes* is, to a certain extent, in favour of Eimer's opinion that there is a close relationship between the first two and between the last two species.

24. Papilio sarpedon: f. 182 to 184.

The ventral portion of the eighth segment covers the vaginal region roof-like. The intersegmental membrane bears a vertical strong fold (*f*), and there is between the fold and the vaginal orifice a strongly chitinised, smooth, impression (*i*). The margin of the orifice of the vagina is slightly raised laterally and produced ventrally into a process (*a*), the form of which will be seen from f. 183, which represents the organ viewed from the dorsal side. F. 182 and 183 are drawn from a Japanese individual. F. 184 is taken from a specimen of *P. sarpedon choredon* from Queensland; the process is broader at the base, and the angles at the apical sinus are more rounded; the difference between f. 183 and 184 is slight, but seems to be fairly constant. We have not found any difference between the processes of *P. sarpedon sarpedon*, *sarpedon semifasciatus*, *sarpedon teredon*, and *sarpedon milon* (!). The individual variation in the form of the process is extremely slight in the specimens examined.

25. Papilio aristeus: f. 185 and 186.

We have examined some Queenslandian *females* of *P. aristeus parmatus*, and a *female* of *P. aristeus hermocrates* from Kalao (between Celebes and Flores); both subspecies agree in the form of the eighth segment and in the genital armature, but in *hermocrates* the outline of the ventral (median) piece of the summit is indicated by a fine ridge. F. 185 and 186 are taken from a Queensland example.

The vaginal armature consists of two chitinised lappets (f. 186, *a* and a^1) which protrude ventrally, and of which the lateral edge runs upwards as a strong ridge, which is homologous to the vertical fold of f. 182, to the ventral margin of the eighth segment.

26. Papilio macfarlanei; f. 187 and 188.

At each side of the vagina there is a broad and strongly chitinised ridge (*f*), homologous to the vertical fold of f. 182, and bearing on the upperside a covering of irregularly folded small lappets. The margin of the vaginal orifice is ventrally produced into a bifurcate process (*a* in f. 187 and 188) which corresponds to the two lappets of fig. 186.

27. Papilio agamemnon; f. 189.

The apparatus is similar to that of *P. macfarlanei*, but the fork-like process has no stem and is connected with the folded intersegmental membrane (*n*) by a short bar visible in f. 189 between the two branches of the fork. We have not noticed any variability in the armature of this species.

Though our researches on the genital armature of the *female* sex of *Papilio* are quite incomplete, we are nevertheless justified in drawing some general conclusions from the facts of variation illustrated by f. 156 to 189.

(1) The prehensile apparatus consists of the armature of the orifice of the vagina, and the special folding of the intersegmental membrane.

connection of the lateral plates of the summit in *podalirius*, *mandarinus*, *ajax*, *leosthenes* is, to a certain extent, in favour of Eimer's opinion that there is a close relationship between the first two and between the last two species.

24. **Papilio sarpedon**: f. 182 to 184.

The ventral portion of the eighth segment covers the vaginal region roof-like. The intersegmental membrane bears a vertical strong fold (*f*), and there is between the fold and the vaginal orifice a strongly chitinised, smooth, impression (*i*). The margin of the orifice of the vagina is slightly raised laterally and produced ventrally into a process (*a*), the form of which will be seen from f. 183, which represents the organ viewed from the dorsal side. F. 182 and 183 are drawn from a Japanese individual. F. 184 is taken from a specimen of *P. sarpedon choredon* from Queensland; the process is broader at the base, and the angles at the apical sinus are more rounded; the difference between f. 183 and 184 is slight, but seems to be fairly constant. We have not found any difference between the processes of *P. sarpedon sarpedon*, *sarpedon semifasciatus*, *sarpedon teredon*, and *sarpedon milon* (!). The individual variation in the form of the process is extremely slight in the specimens examined.

25. **Papilio aristeus**: f. 185 and 186.

We have examined some Queenslandian *females* of *P. aristeus parmatus*, and a *female* of *P. aristeus hermocrates* from Kalao (between Celebes and Flores); both subspecies agree in the form of the eighth segment and in the genital armature, but in *hermocrates* the outline of the ventral (median) piece of the summit is indicated by a fine ridge. F. 185 and 186 are taken from a Queensland example.

The vaginal armature consists of two chitinised lappets (f. 186, *a* and *a*^{1}) which protrude ventrally, and of which the lateral edge runs upwards as a strong ridge, which is homologous to the vertical fold of f. 182, to the ventral margin of the eighth segment.

26. **Papilio macfarlanei**; f. 187 and 188.

At each side of the vagina there is a broad and strongly chitinised ridge (*f*), homologous to the vertical fold of f. 182, and bearing on the upperside a covering of irregularly folded small lappets. The margin of the vaginal orifice is ventrally produced into a bifurcate process (*a* in f. 187 and 188) which corresponds to the two lappets of fig. 186.

27. **Papilio agamemnon**; f. 189.

The apparatus is similar to that of *P. macfarlanei*, but the fork-like process has no stem and is connected with the folded intersegmental membrane (*n*) by a short bar visible in f. 189 between the two branches of the fork. We have not noticed any variability in the armature of this species.

Though our researches on the genital armature of the *female* sex of *Papilio* are quite incomplete, we are nevertheless justified in drawing some general conclusions from the facts of variation illustrated by f. 156 to 189.

(1) The prehensile apparatus consists of the armature of the orifice of the vagina, and the special folding of the intersegmental membrane.

(2) The folds of the intersegmental membrane cannot be studied from the dried-up individuals in such a manner that one perceives the minute differences between the folds of the individuals; to this purpose it is necessary to compare live specimens, or material preserved in an adequate fluid. The armature of the valve of the *male* is during copulation pressed against the intersegmental membrane of the *female*, and the spines, hooks, processes, etc., of the valve find a hold on the ridge-like folds of the intersegmental membrane ; this is plainly visible in a ♂ and ♀ of *P. memnon* in the Tring Museum which are still united to one another. The special armature of the vagina takes hold on the internal portion of the ninth segment of the *male* and on the scaphium. There is sometimes a peculiarly shaped, broad, vertical, chitinous plate underneath the scaphium, for example in the *males* of the yellow *Troides* (= *Ornithoptera*), such as *T. helenus*, to which a long and strong ventral hook in the *female* corresponds.

(3) One would expect that the variation of the harpe in the *male* is in the same species accompanied by a corresponding variation in the *female* in those parts which during copulation are in contact with the harpe ; hence the variation in the *female* genital apparatus parallel to the variation in the *male* harpe must be searched for in the special kind of folding of the intersegmental membrane, while the variation in the outline of the processes and ridges at the mouth of the vagina can have nothing to do with an adaptation to the special form of the harpe.

(4) In the only species examined in which the harpes vary very conspicuously according to locality, in *P. alcinous*, the intersegmental fold of the ♀ on which the harpe takes a hold is found to be different in the Chinese and the Japanese subspecies.

(5) Though the individual variation of the vaginal armature is often great (*P. aegeus* and *memnon*), a variation according to locality is not observed, or is slight.

(6) In species with polymorphic *females* the vaginal armature is the same in the various *females* (apart from individual variability).

III.—CONCLUSIONS.

The demonstration of the kind and the extent of the variation of the genital armature in both sexes of some species of *Papilio* which is contained in the preceding chapter, notwithstanding the fact that our researches are still incomplete and our notes on the vaginal apparatus even preliminary, enables us to compare the variation of the genital armature with that of other organs and to draw with safety some general conclusions. If we almost restrict the comparison to the colour, pattern, and shape of the wings, mentioning only the prominent characters of the respective insects, we do so in order to avoid unnecessary detail, and secondly, because the distinguishing characters of species, subspecies, and aberrations of butterflies as given in the works of Lepidopterists refer especially to the wings.

As the true basis of work in Natural History is the comparison of specimen with specimen of the lowest classificatory entity, the species, a study of the genital armature has to begin with the comparison of the armature of such individuals as are doubtless specifically the same. To determine the limits of variation of the genital armature of a species is a difficult task. Though the number of specimens of the commoner species could easily be enlarged without any great

(2) The folds of the intersegmental membrane cannot be studied from the dried-up individuals in such a manner that one perceives the minute differences between the folds of the individuals; to this purpose it is necessary to compare live specimens, or material preserved in an adequate fluid. The armature of the valve of the *male* is during copulation pressed against the intersegmental membrane of the *female*, and the spines, hooks, processes, etc., of the valve find a hold on the ridge-like folds of the intersegmental membrane; this is plainly visible in a ♂ and ♀ of *P. memnon* in the Tring Museum which are still united to one another. The special armature of the vagina takes hold on the internal portion of the ninth segment of the *male* and on the scaphium. There is sometimes a peculiarly shaped, broad, vertical, chitinous plate underneath the scaphium, for example in the *males* of the yellow *Troides* (= *Ornithoptera*), such as *T. helenus*, to which a long and strong ventral hook in the *female* corresponds.

(3) One would expect that the variation of the harpe in the *male* is in the same species accompanied by a corresponding variation in the *female* in those parts which during copulation are in contact with the harpe; hence the variation in the *female* genital apparatus parallel to the variation in the *male* harpe must be searched for in the special kind of folding of the intersegmental membrane, while the variation in the outline of the processes and ridges at the mouth of the vagina can have nothing to do with an adaptation to the special form of the harpe.

(4) In the only species examined in which the harpes vary very conspicuously according to locality, in *P. alcinous*, the intersegmental fold of the ♀ on which the harpe takes a hold is found to be different in the Chinese and the Japanese subspecies.

(5) Though the individual variation of the vaginal armature is often great (*P. aegeus* and *memnon*), a variation according to locality is not observed, or is slight.

(6) In species with polymorphic *females* the vaginal armature is the same in the various *females* (apart from individual variability).

III.—CONCLUSIONS.

The demonstration of the kind and the extent of the variation of the genital armature in both sexes of some species of *Papilio* which is contained in the preceding chapter, notwithstanding the fact that our researches are still incomplete and our notes on the vaginal apparatus even preliminary, enables us to compare the variation of the genital armature with that of other organs and to draw with safety some general conclusions. If we almost restrict the comparison to the colour, pattern, and shape of the wings, mentioning only the prominent characters of the respective insects, we do so in order to avoid unnecessary detail, and secondly, because the distinguishing characters of species, subspecies, and aberrations of butterflies as given in the works of Lepidopterists refer especially to the wings.

As the true basis of work in Natural History is the comparison of specimen with specimen of the lowest classificatory entity, the species, a study of the genital armature has to begin with the comparison of the armature of such individuals as are doubtless specifically the same. To determine the limits of variation of the genital armature of a species is a difficult task. Though the number of specimens of the commoner species could easily be enlarged without any great pecuniary sacrifice, the student of the variation of an internal organ, which is not visible without dissection, is at a great disadvantage compared with the student of external characters, because his series of individuals is always taken at random ; he has no security whatever that, among the hundreds of specimens which perhaps are at his disposal, there are really individuals which in the genital armature represent the extremes of that species, or come near the extremes ; while, on the other hand, the specimens conspicuously aberrant in wing-pattern, or colour, or shape, are recognised and preserved by collectors, which gradually results in an accumulation of individuals which fairly represent the various degrees, inclusive of the more extreme ones, of the variation of the species in external characters. Hence it is by no means to be wondered at that there are so many individuals known which in external characters stand far outside the *usual* limits of variation of the respective species, while the internal genital armature seemed to vary only within very narrow limits. On the contrary, it must surprise us that we nevertheless *did* succeed in finding among our specimens such individuals as exhibit in the genital organs characters so widely divergent from the normal of the respective race of *Papilio* that the individual not only forms a transition to another geographical representative, but goes in the development of the peculiar character even beyond allied forms. The specimen of *P. sarpedon sarpedon* (f. 101, 102, 103) and those of *P. alcinous* figured on Pl. VI. of Vol. II. of this journal (f. 11 and 13) are such "unusual" varieties, which perhaps are in nature not rarer than individuals that in external characters come close to, or are identical with, one of the allied forms; and we have no doubt that a continued investigation in the matter will bring to light varieties in the genital armature which in the degree of divergency are equal to so-called sports. The individual variability found in our series of British *P. machaon* to amount to 40 per cent. in the gradual increase of the length of the prehensile portion of the harpe, and in Palaearctic *machaon* to 70 per cent., is quantitatively scarcely inferior to the variation exhibited in external characters, and the same applies to the other Papilios dealt with in the preceding chapter. In the *female* genital armature we meet with an equally great variability in many of the species, especially in all those which have a more complicated armature ; the variability of the complicated apparatus, which consists of spines, hooks, dentate ridges, and so on, appears generally to be greater than that of a simpler armature, because the difference between the apparatus of two individuals is more easily perceivable in a complicated than in a simple organ, even if the difference in the latter expressed in proportional numbers is greater than in the former.

If we group the individuals of a species from one locality according to the similarity in the genital armature, and then again according to a conspicuous external character, the first series of groups and the second are not the same ; we have found again and again that specimens similar in a certain character in colour, pattern, or shape of wings have no particularity in the genital armature in common by which they are distinguished from the individuals that do not possess that external character ; specimens aberrant in wing-pattern may be normal in the genital armature, and individuals abnormal in the latter may be normal in the former. The harpe of *P. aegeus ormenus* with a band on the forewing is the same as in the aberration without the band ; *P. euchenor euchenor* ab. *eutropius* does not differ in the harpe from the ordinary *male* ; *P. polytes borealis* ab. *thibetanus* has a normal harpe, and so on. Still more obvious is the independence of the variation of the genital armature in the species with polymorphic *females* ; the various *females* pecuniary sacrifice, the student of the variation of an internal organ, which is not visible without dissection, is at a great disadvantage compared with the student of external characters, because his series of individuals is always taken at random; he has no security whatever that, among the hundreds of specimens which perhaps are at his disposal, there are really individuals which in the genital armature represent the extremes of that species, or come near the extremes; while, on the other hand, the specimens conspicuously aberrant in wing-pattern, or colour, or shape, are recognised and preserved by collectors, which gradually results in an accumulation of individuals which fairly represent the various degrees, inclusive of the more extreme ones, of the variation of the species in external characters. Hence it is by no means to be wondered at that there are so many individuals known which in external characters stand far outside the *usual* limits of variation of the respective species, while the internal genital armature seemed to vary only within very narrow limits. On the contrary, it must surprise us that we nevertheless *did* succeed in finding among our specimens such individuals as exhibit in the genital organs characters so widely divergent from the normal of the respective race of *Papilio* that the individual not only forms a transition to another geographical representative, but goes in the development of the peculiar character even beyond allied forms. The specimen of *P. sarpedon sarpedon* (f. 101, 102, 103) and those of *P. alcinous* figured on Pl. VI. of Vol. II. of this journal (f. 11 and 13) are such "unusual" varieties, which perhaps are in nature not rarer than individuals that in external characters come close to, or are identical with, one of the allied forms; and we have no doubt that a continued investigation in the matter will bring to light varieties in the genital armature which in the degree of divergency are equal to so-called sports. The individual variability found in our series of British *P. machaon* to amount to 40 per cent. in the gradual increase of the length of the prehensile portion of the harpe, and in Palaearctic *machaon* to 70 per cent., is quantitatively scarcely inferior to the variation exhibited in external characters, and the same applies to the other Papilios dealt with in the preceding chapter. In the *female* genital armature we meet with an equally great variability in many of the species, especially in all those which have a more complicated armature; the variability of the complicated apparatus, which consists of spines, hooks, dentate ridges, and so on, appears generally to be greater than that of a simpler armature, because the difference between the apparatus of two individuals is more easily perceivable in a complicated than in a simple organ, even if the difference in the latter expressed in proportional numbers is greater than in the former.

If we group the individuals of a species from one locality according to the similarity in the genital armature, and then again according to a conspicuous external character, the first series of groups and the second are not the same; we have found again and again that specimens similar in a certain character in colour, pattern, or shape of wings have no particularity in the genital armature in common by which they are distinguished from the individuals that do not possess that external character; specimens aberrant in wing-pattern may be normal in the genital armature, and individuals abnormal in the latter may be normal in the former. The harpe of *P. aegeus ormenus* with a band on the forewing is the same as in the aberration without the band; *P. euchenor euchenor* ab. *eutropius* does not differ in the harpe from the ordinary *male*; *P. polytes borealis* ab. *thibetanus* has a normal harpe, and so on. Still more obvious is the independence of the variation of the genital armature in the species with polymorphic *females*; the various *females* of *memnon*, tailed and tailless, those of *polytes*, and also those of *aegeus ormenus*, though individually very variable in the vaginal armature, agree with one another (respectively) in these organs. Marked dimorphism, in which the two forms are not connected by intergradations (tailed and tailless *female* of *P. memnon*), we have not noticed in the genital armature, unless f. 171 and 173, in which the lateral ridge is not divided, and f. 174 and 175, in which the lateral ridge is divided into the two ridges *o* and *u*, represent a kind of dimorphism; both the simple and the divided ridge occur in tailed as well as in tailless individuals of *P. memnon*; intergradations between the two developments of the lateral ridge are unknown to us, but may occur.

Of equally great interest are those cases in which a specimen of a certain subspecies resembles another subspecies externally, but stands further away from this subspecies in the genital armature than another specimen does that externally is dissimilar to the subspecies. We recall to mind the two individuals of *P. aristeus hermocrates* from the Shan States mentioned on p. 487, and add that, if variation in pattern and variation in the sexual organs were in any way connected with one another, one would have expected that the paler individual resembling certain Sikkim specimens of *anticrates* had the dorsal lobe of the valve broader than the other individual, which in pattern is like dark Philippine examples; as, however, just the reverse is the case, the broader dorsal lobe of the valve and the narrower and shorter black bands of *anticrates*, and the narrower dorsal lobe and more extended black bands of *hermocrates*, must be considered as independent characters.

It is possible that there are species in which a great variability, resp. constancy, of the pattern of the wing is associated with a great variability, resp. constancy, in the sexual armature, but so much is certain that in all the species we have examined there is no correlation between the directions in which the wings and the sexual armature vary. Hence we may pronounce it as a general law *that the direction of the variation of the genital armature within a species of Papilio is entirely independent of the variation of the wings.*

We need scarcely mention that this law applies also to other *Lepidoptera*; our researches in groups other than *Papilio* are, however, so limited that we prefer for the present to express the law as above. It would be of great interest to study the variation of the genital armature of specimens which have artificially been exposed to transmuting factors, such as heat and cold, and to compare the results with those arrived at by the examination of the individuals roaming at large. Most probably the artificially produced colour-varieties will be normal in the genital armature. To this conclusion we are led by the experience gained from the examination of seasonally dimorphic species. We paid special attention to the copulatory apparatus of such species with the hope of finding in one or the other *Papilio* differences in the apparatus of the spring and summer brood (or broods), but completely failed to come across a species which, both in the wing-markings and in the sexual organs, showed seasonal dimorphism. The spring forms of the Japanese *P. machaon*, *P. xuthus*, and *P. sarpedon* are in the harpe and the vaginal armature the same as the differently coloured respective summer forms, and so it is with the Sikkimese species which exhibit in the wings a marked seasonal dimorphism (*P. sarpedon*, *cloanthus*, *eurypylus*, *bathycles*). In the case of winter and summer forms it is therefore evident that the influences which bring about a change in the wings have no apparent effect on the sexual armature. This corroborates the above statement of the independence of the variation of the sexual of *memnon*, tailed and tailless, those of *polytes*, and also those of *aegeus ormenus*, though individually very variable in the vaginal armature, agree with one another (respectively) in these organs. Marked dimorphism, in which the two forms are not connected by intergradations (tailed and tailless *female* of *P. memnon*), we have not noticed in the genital armature, unless f. 171 and 173, in which the lateral ridge is not divided, and f. 174 and 175, in which the lateral ridge is divided into the two ridges *o* and *u*, represent a kind of dimorphism; both the simple and the divided ridge occur in tailed as well as in tailless individuals of *P. memnon*; intergradations between the two developments of the lateral ridge are unknown to us, but may occur.

Of equally great interest are those cases in which a specimen of a certain subspecies resembles another subspecies externally, but stands further away from this subspecies in the genital armature than another specimen does that externally is dissimilar to the subspecies. We recall to mind the two individuals of *P. aristeus hermocrates* from the Shan States mentioned on p. 487, and add that, if variation in pattern and variation in the sexual organs were in any way connected with one another, one would have expected that the paler individual resembling certain Sikkim specimens of *anticrates* had the dorsal lobe of the valve broader than the other individual, which in pattern is like dark Philippine examples; as, however, just the reverse is the case, the broader dorsal lobe of the valve and the narrower and shorter black bands of *anticrates*, and the narrower dorsal lobe and more extended black bands of *hermocrates*, must be considered as independent characters.

It is possible that there are species in which a great variability, resp. constancy, of the pattern of the wing is associated with a great variability, resp. constancy, in the sexual armature, but so much is certain that in all the species we have examined there is no correlation between the directions in which the wings and the sexual armature vary. Hence we may pronounce it as a general law *that the direction of the variation of the genital armature within a species of Papilio is entirely independent of the variation of the wings.*

We need scarcely mention that this law applies also to other *Lepidoptera*; our researches in groups other than *Papilio* are, however, so limited that we prefer for the present to express the law as above. It would be of great interest to study the variation of the genital armature of specimens which have artificially been exposed to transmuting factors, such as heat and cold, and to compare the results with those arrived at by the examination of the individuals roaming at large. Most probably the artificially produced colour-varieties will be normal in the genital armature. To this conclusion we are led by the experience gained from the examination of seasonally dimorphic species. We paid special attention to the copulatory apparatus of such species with the hope of finding in one or the other *Papilio* differences in the apparatus of the spring and summer brood (or broods), but completely failed to come across a species which, both in the wing-markings and in the sexual organs, showed seasonal dimorphism. The spring forms of the Japanese *P. machaon*, *P. xuthus*, and *P. sarpedon* are in the harpe and the vaginal armature the same as the differently coloured respective summer forms, and so it is with the Sikkimese species which exhibit in the wings a marked seasonal dimorphism (*P. sarpedon*, *cloanthus*, *eurypylus*, *bathycles*). In the case of winter and summer forms it is therefore evident that the influences which bring about a change in the wings have no apparent effect on the sexual armature. This corroborates the above statement of the independence of the variation of the sexual organs and the wing-pattern, and opens a wide field for theoretical research, inviting at the same time to a comparison of the seasonal with the geographical variation.

In the introduction we have mentioned the degrees of geographical variation observed in Papilios ; the lower degrees, called above localised aberration, concern the colour, pattern, and shape of the wings, and cannot be expected to be noticeable in the genital armature without long-continued research; we have therefore to do only with the higher degrees of geographical variation of a species which is termed *subspecific* variation.

The valve, when of the usual more or less triangular outline, does not exhibit obvious subspecific variation; while the variation according to locality is conspicuous, when the valve is divided into lobes, as is the case in *P. sarpedon*, *aristeus*, and others. The variation is such that the specimens from a certain locality are generally well distinguished from the specimens of a certain other locality; but if we take individuals from all the various districts inhabited by the respective species, the lines of delimitation of the various forms become mostly obscure and disappear. North Indian specimens of *sarpedon* and individuals from Sambawa are at once distinguished by the form of the valval lobes, but examples from Lombok, Java, and Sumatra overbridge the gap; Queenslandian and Sikkim *aristeus* are in the dorsal lobe of the valve quite dissimilar, but specimens from the interjacent countries form a continuous series of intergradations between those two extremes. The armature of the valve varies in a similar way. We have cases in which the prehensile organ of part of the individuals of the various localities has some peculiarity; thus in Great Britain the prehensile portion of the harpe of a good many specimens of *P. machaon* is long, while in many individuals from Syria the dentate portion is very short ; the subspecific difference in the harpe of *P. aegeus* from New Guinea and Australia is very slight and applies only to part of the specimens. In other species the differences between the individuals from various districts become more constant, so that with very few exceptions it is possible to tell from the examination of the harpe from which place a respective specimen came. While in other cases again, such as *P. bathycles*, the individuals examined were constantly different in the harpe according to locality.

The localised peculiarity in the harpe is, therefore, found in many, or in nearly all, or in all the individuals from the respective locality, and when the distinguishing character applies to all the specimens, there occur intergradations either in other places (*P. aristeus*), or intergradations are unknown (*P. bathycles*).

In the *female* sex the armature at the mouth of the vagina does not vary so obviously according to locality as the harpe of the *male* does ; but when the difference in the harpes of the subspecies is very conspicuous, as in *P. alcinous alcinous* and *P. alcinous confusus*, the difference in the corresponding part of the vaginal bulb is also prominent.

If we keep in mind that the variation of the copulatory organs is independent of the variation of the wing-characters, it is to be expected that a division of a species into subspecies will result in a different number of subspecies according as we take for the basis of division solely the wing-characters, or the genital armature, or both united; and it would likewise not be surprising if in a certain case the number of subspecies inhabiting a certain region would by both divisions be the same, but the lines of division be different. Among the species we have examined the latter phenomenon did not occur ; when the numbers of the subspecies organs and the wing-pattern, and opens a wide field for theoretical research, inviting at the same time to a comparison of the seasonal with the geographical variation.

In the introduction we have mentioned the degrees of geographical variation observed in Papilios; the lower degrees, called above localised aberration, concern the colour, pattern, and shape of the wings, and cannot be expected to be noticeable in the genital armature without long-continued research; we have therefore to do only with the higher degrees of geographical variation of a species which is termed *subspecific* variation.

The valve, when of the usual more or less triangular outline, does not exhibit obvious subspecific variation; while the variation according to locality is conspicuous, when the valve is divided into lobes, as is the case in *P. sarpedon*, *aristeus*, and others. The variation is such that the specimens from a certain locality are generally well distinguished from the specimens of a certain other locality; but if we take individuals from all the various districts inhabited by the respective species, the lines of delimitation of the various forms become mostly obscure and disappear. North Indian specimens of *sarpedon* and individuals from Sambawa are at once distinguished by the form of the valval lobes, but examples from Lombok, Java, and Sumatra overbridge the gap; Queenslandian and Sikkim *aristeus* are in the dorsal lobe of the valve quite dissimilar, but specimens from the interjacent countries form a continuous series of intergradations between those two extremes. The armature of the valve varies in a similar way. We have cases in which the prehensile organ of part of the individuals of the various localities has some peculiarity; thus in Great Britain the prehensile portion of the harpe of a good many specimens of *P. machaon* is long, while in many individuals from Syria the dentate portion is very short; the subspecific difference in the harpe of *P. aegeus* from New Guinea and Australia is very slight and applies only to part of the specimens. In other species the differences between the individuals from various districts become more constant, so that with very few exceptions it is possible to tell from the examination of the harpe from which place a respective specimen came. While in other cases again, such as *P. bathycles*, the individuals examined were constantly different in the harpe according to locality.

The localised peculiarity in the harpe is, therefore, found in many, or in nearly all, or in all the individuals from the respective locality, and when the distinguishing character applies to all the specimens, there occur intergradations either in other places (*P. aristeus*), or intergradations are unknown (*P. bathycles*).

In the *female* sex the armature at the mouth of the vagina does not vary so obviously according to locality as the harpe of the *male* does; but when the difference in the harpes of the subspecies is very conspicuous, as in *P. alcinous alcinous* and *P. alcinous confusus*, the difference in the corresponding part of the vaginal bulb is also prominent.

If we keep in mind that the variation of the copulatory organs is independent of the variation of the wing-characters, it is to be expected that a division of a species into subspecies will result in a different number of subspecies according as we take for the basis of division solely the wing-characters, or the genital armature, or both united; and it would likewise not be surprising if in a certain case the number of subspecies inhabiting a certain region would by both divisions be the same, but the lines of division be different. Among the species we have examined the latter phenomenon did not occur; when the numbers of the subspecies were the same, the limits of division were also the same, whether the delimitation of each subspecies was carried out according to the wing-characters, or according to the apparatus of copulation. This result is most probably owing to the areas to which the various subspecies of the Papilios examined are restricted being mostly islands.

Hence we can accept it as a general rule applying to most subspecies that the distinguishing characters taken from the wings are associated with distinguishing characters in the genital armature, at least in the *male* sex. There are, however, many exceptions to this rule, in so far as a good number of subspecies characterised by some certain peculiarity in the wings have no peculiarity in the apparatus of copulation. The Chinese specimens of *P. sarpedon*, so very conspicuously aberrant in pattern, are in the valve and harpe identical with the Indian and Japanese form of *sarpedon*; the Moluccan subspecies of *P. aristeus*, though in the extent of the markings very different from the Queenslandian representative, is in the sexual organs the same; so that in an arrangement of the forms according to the development of the apparatus of copulation of the *male*, *P. aristeus aristeus* and *P. aristeus parmatus*, and *P. sarpedon sarpedon* and *P. sarpedon semifasciatus*, would have to be united. We meet, further, many subspecies which in external characters are conspicuously and almost constantly different, while there is only a slight and very inconstant character of distinction in the genital apparatus. We have found it correct in all the species examined that, if in a given species the character of distinction of a certain subspecies lies in one only of two independently varying organs, wings and apparatus of copulation, it is invariably the wing which exhibits the character by which the subspecies is distinguished. This coincides in a remarkable manner with the above observation that seasonal dimorphism does not affect the sexual armature in the case of the North Indian and Japanese Papilios, and renders it certain that the effect of (seasonally or geographically) isolated transmuting factors is first noticeable in the wing-markings, and that accordingly the transmutation of a species begins with a change in the wing-markings. Hence it is also correct to say that in an evolutionistic sense the wing-markings are less constant than the genital armature, and that consequently a difference in the latter constantly met with in the individuals of two forms of *Papilio* is much more likely to be of specific value than a difference in the wing-pattern, a conclusion which borders closely upon one of the main objects of our researches, the question as to the classificatory value of the sexual armature, which we will now briefly discuss.

d. TAXONOMIC VALUE OF THE ORGANS OF COPULATION.

As our researches have proved that there is a certain amount of individual variation in the sexual armature, the limits of which can, as we have seen above, only be determined by continued examination of a large material, and as we further have found that there is geographical polymorphism in the organs in question in which the localised forms are connected by intergradations (*P. sarpedon sarpedon* and *adonarensis*, *P. aristeus hermocrates* and *anticrates*), the premisses of the discussion of the question which characters are and which are not of specific value are precisely the same as in the case of external characters. Referring to what we have said in the introduction about our means of recognition of specific distinctness, it will be sufficient to recall to mind the fact that the presence of a character in a certain form not met with in other forms is *a priori* not a proof of the respective form being were the same, the limits of division were also the same, whether the delimitation of each subspecies was carried out according to the wing-characters, or according to the apparatus of copulation. This result is most probably owing to the areas to which the various subspecies of the Papilios examined are restricted being mostly islands.

Hence we can accept it as a general rule applying to most subspecies that the distinguishing characters taken from the wings are associated with distinguishing characters in the genital armature, at least in the *male* sex. There are, however, many exceptions to this rule, in so far as a good number of subspecies characterised by some certain peculiarity in the wings have no peculiarity in the apparatus of copulation. The Chinese specimens of *P. sarpedon*, so very conspicuously aberrant in pattern, are in the valve and harpe identical with the Indian and Japanese form of *sarpedon*; the Moluccan subspecies of *P. aristeus*, though in the extent of the markings very different from the Queenslandian representative, is in the sexual organs the same; so that in an arrangement of the forms according to the development of the apparatus of copulation of the *male*, *P. aristeus aristeus* and *P. aristeus parmatus*, and *P. sarpedon sarpedon* and *P. sarpedon semifasciatus*, would have to be united. We meet, further, many subspecies which in external characters are conspicuously and almost constantly different, while there is only a slight and very inconstant character of distinction in the genital apparatus. We have found it correct in all the species examined that, if in a given species the character of distinction of a certain subspecies lies in one only of two independently varying organs, wings and apparatus of copulation, it is invariably the wing which exhibits the character by which the subspecies is distinguished. This coincides in a remarkable manner with the above observation that seasonal dimorphism does not affect the sexual armature in the case of the North Indian and Japanese Papilios, and renders it certain that the effect of (seasonally or geographically) isolated transmuting factors is first noticeable in the wing-markings, and that accordingly the transmutation of a species begins with a change in the wing-markings. Hence it is also correct to say that in an evolutionistic sense the wing-markings are less constant than the genital armature, and that consequently a difference in the latter constantly met with in the individuals of two forms of *Papilio* is much more likely to be of specific value than a difference in the wing-pattern, a conclusion which borders closely upon one of the main objects of our researches, the question as to the classificatory value of the sexual armature, which we will now briefly discuss.

d. TAXONOMIC VALUE OF THE ORGANS OF COPULATION.

As our researches have proved that there is a certain amount of individual variation in the sexual armature, the limits of which can, as we have seen above, only be determined by continued examination of a large material, and as we further have found that there is geographical polymorphism in the organs in question in which the localised forms are connected by intergradations (*P. sarpedon sarpedon* and *adonarensis*, *P. aristeus hermocrates* and *anticrates*), the premisses of the discussion of the question which characters are and which are not of specific value are precisely the same as in the case of external characters. Referring to what we have said in the introduction about our means of recognition of specific distinctness, it will be sufficient to recall to mind the fact that the presence of a character in a certain form not met with in other forms is *a priori* not a proof of the respective form being specifically distinct from its allies, and that it is circumstantial evidence which has to guide us, in the absence of experiments, in our judgment. Now, what is the evidence we derive from the examination of the organs of copulation?

We know the larval and imaginal state of a good many Papilios, and are able to base on our knowledge of their organisation, quite apart from the characters of the organs of copulation, a classification in which the most nearly allied species are, with a certain degree of correctness, grouped together. If we now compare of a well-studied group such forms about the specific distinctness of which we do not entertain any doubt—if, for example, we examine the sexual armature of *P. memnon*, *mayo*, *oenomaus*, *polymnestor*, *lampsacus*, *rumanzovius*, etc., which in their general organisation are all more or less closely allied to *P. memnon*, or take for examination *P. antiphates* and *androcles*, or *P. aristolochiae* and *P. polydorus*, or the various yellow species of *Troides* (= *Ornithoptera*)—the first thing we notice is that the imagines of each species exhibit, besides the distinguishing characters in colour and structure externally visible, also characters in the genital armature peculiar to the respective species. As we have not found amongst all those species the specific distinctness of which we could deduce from characters other than such of the organs of copulation a single exception to that rule, we hope we are justified in generalising the statement that every species of *Papilio* is different from every other species in the sexual armature: and this generalisation we believe the more confidently to be correct as also in other groups of *Lepidoptera* specifically distinct forms are characterised by some peculiarity in the copulatory organs, although the difference between allied species is sometimes—for example, among *Aganaidae*—very slight. If the generalisation is correct—*i.e.* if every form that is, according to our definition of the term "species," specifically distinct, which, we repeat, can only be *proved* by experiment, and we will assume the generalisation to be correct—then it follows necessarily that forms which are identical in the genital armature are also specifically identical. If we apply this conclusion to the species of *Papilio* externally polymorphic, it is evident that the genital armature of *male* and *female* is an excellent criterion of specific identity. The various varieties of the *male* of *P. aegeus ormenus* from New Guinea, of *Troides priamus poseidon* from the same country, of *P. memnon*, and so on, many of which have been described as distinct species, are thus easily demonstrated to be specifically the same. Still more important is the application to the *female* sex. The numerous species with polymorphic *females* which so often are quite unlike each other, as in the case of *P. memnon*, *P. aegeus ormenus*, *P. polytes*, and the African *P. phorcas* and *merope*, and some American species—an examination of the genital apparatus of a number of specimens will at once make it clear whether the forms in question belong certainly to one species, or whether they eventually can belong to more species. We say intentionally "a number of specimens," for the examination of one example of each form is quite inadequate, and may lead to entirely erroneous conclusions. F. 171 and 173 give an excellent illustration, the first being taken from a tailless example of *P. memnon agenor* from Sikkim, and the other from a tailed specimen from the same locality. Now, considering that f. 167 represents a species very different from *memnon*, it would by no means be preposterous to conclude, if one had to judge only from the three figures and the conspicuous external differences of the specimens, that f. 171 and 173 represented likewise specifically different Papilios. It will generally be quite sufficient to examine a number of individuals of one of the forms, and to determine thus the probable limits of variation; the vaginal apparatus specifically distinct from its allies, and that it is circumstantial evidence which has to guide us, in the absence of experiments, in our judgment. Now, what is the evidence we derive from the examination of the organs of copulation?

We know the larval and imaginal state of a good many Papilios, and are able to base on our knowledge of their organisation, quite apart from the characters of the organs of copulation, a classification in which the most nearly allied species are, with a certain degree of correctness, grouped together. If we now compare of a well-studied group such forms about the specific distinctness of which we do not entertain any doubt—if, for example, we examine the sexual armature of *P. memnon*, *mayo*, *oenomaus*, *polymnestor*, *lampsacus*, *rumanzorius*, etc., which in their general organisation are all more or less closely allied to *P. memnon*, or take for examination *P. antiphates* and *androcles*, or *P. aristolochiae* and *P. polydorus*, or the various yellow species of *Troides* (= *Ornithoptera*)—the first thing we notice is that the imagines of each species exhibit, besides the distinguishing characters in colour and structure externally visible, also characters in the genital armature peculiar to the respective species. As we have not found amongst all those species the specific distinctness of which we could deduce from characters other than such of the organs of copulation a single exception to that rule, we hope we are justified in generalising the statement that every species of *Papilio* is different from every other species in the sexual armature: and this generalisation we believe the more confidently to be correct as also in other groups of *Lepidoptera* specifically distinct forms are characterised by some peculiarity in the copulatory organs, although the difference between allied species is sometimes—for example, among *Aganaidae*—very slight. If the generalisation is correct—*i.e.* if every form that is, according to our definition of the term "species," specifically distinct, which, we repeat, can only be *proved* by experiment, and we will assume the generalisation to be correct—then it follows necessarily that forms which are identical in the genital armature are also specifically identical. If we apply this conclusion to the species of *Papilio* externally polymorphic, it is evident that the genital armature of *male* and *female* is an excellent criterion of specific identity. The various varieties of the *male* of *P. aegeus ormenus* from New Guinea, of *Troides priamus poseidon* from the same country, of *P. memnon*, and so on, many of which have been described as distinct species, are thus easily demonstrated to be specifically the same. Still more important is the application to the *female* sex. The numerous species with polymorphic *females* which so often are quite unlike each other, as in the case of *P. memnon*, *P. aegeus ormenus*, *P. polytes*, and the African *P. phorcas* and *merope*, and some American species—an examination of the genital apparatus of a number of specimens will at once make it clear whether the forms in question belong certainly to one species, or whether they eventually can belong to more species. We say intentionally "a number of specimens," for the examination of one example of each form is quite inadequate, and may lead to entirely erroneous conclusions. F. 171 and 173 give an excellent illustration, the first being taken from a tailless example of *P. memnon agenor* from Sikkim, and the other from a tailed specimen from the same locality. Now, considering that f. 167 represents a species very different from *memnon*, it would by no means be preposterous to conclude, if one had to judge only from the three figures and the conspicuous external differences of the specimens, that f. 171 and 173 represented likewise specifically different Papilios. It will generally be quite sufficient to examine a number of individuals of one of the forms, and to determine thus the probable limits of variation; the vaginal apparatus of a specimen of another form, if specifically the same as the first, then will most probably come within the limits of variation of the first; if it stands outside those limits one has to examine some more specimens. It is perhaps not unnecessary to repeat that the tailed and tailless *females* of *P. memnon* have been *proved* by rearing to belong to one species.

The second point which strikes one when comparing the sexual armature of species of the same group or closely allied groups, and which is of no less great practical consequence, concerns the fact that the species which we must regard as more or less close relatives on the ground of their general organisation bear in the structure of the organs of copulation (inclusive of the modified eighth segment of the *female*) a greater resemblance to one another than to the species which stand further away in the system. Representative species, such as *P. aristeus* and *rhesus*: *aegeus*, *tydeus*, *gambrisius*, *inopinatus*; *euchenor* and *depilis*, etc., have the organs in question built up after exactly the same plan, and the differences exhibited by these representative species in the organs of copulation are often not only far less obvious than the external differences of the species, but are sometimes so slight that the degree of divergence between two species is less than the degree of divergency between the extreme individuals of one of the two species; we refer for illustration to the figures given of the harpes of *P. aegeus* and *inopinatus*, *polytes* and *ambrax*. In less closely related species the similarity in the sexual armature is not so great as in those representative species which are phylogenetically younger forms; the organs are more divergently developed, and the peculiar modification of one or the other part of the apparatus often obscures the actual homology, so that the organs superficially compared are very dissimilar in appearance. Nevertheless a comparative study at once shows that the superficially dissimilar apparatus are developments of the same type. In *P. sarpedon* and *cloanthus* the close relationship of the valves and harpes (f. 96 and 149) is obvious. In *aristeus* (with *rhesus*, f. 72 to 82) the organs are more strongly modified, but the homology of the single parts with those of *P. cloanthus* is not difficult to perceive: *antiphates* has the organs again similar to those of *aristeus*, and the externally very dissimilar *P. delesserti*, *leucothoë*, and *xenocles* resemble *aristeus* in the structure of the *male* organs to a surprising extent, the principal prehensile parts of the valve consisting in these species, as in *aristeus* and *antiphates*, of a ventral dentate ridge, a subdorsal process, and the dorsal lobe of the bipartite valve, which parts respectively are homologous to *e*, *c*, *b* of f. 72 (*aristeus*). The vaginal armature agrees in this respect with the *male* armature; here again the most closely allied species have a greater similarity in the organs in question to one another than to less nearly related species: *P. ambrax* and *polytes* (f. 161 and 160); *P. aegeus*, *rumanzovius*, and *memnon* (f. 166, 170, and 171); *P. sarpedon*, *aristeus*, *agamemnon*, and *macfarlanei* (f. 182 to 187) illustrate this fact sufficiently. Although it would seem to follow from these statements that the degree of blood-relationship of two species to a third could easily be made out from the degree of similarity in the form of their organs of copulation, this inference of the facts would nevertheless be hasty and most probably erroneous, if we generalised the conclusion so as to apply to every species. Our researches convince us that it is true that in every group of closely allied species of *Papilio* the characters of the three independently variable organs, wing, harpe of *male*, and the vaginal armature of *female*, are such that each of these organs of every species is morphologically closer related to the respective organ of every other species of the group than to that of any species standing outside the group.

of a specimen of another form, if specifically the same as the first, then will most probably come within the limits of variation of the first; if it stands outside those limits one has to examine some more specimens. It is perhaps not unnecessary to repeat that the tailed and tailless *females* of *P. memnon* have been *proved* by rearing to belong to one species.

The second point which strikes one when comparing the sexual armature of species of the same group or closely allied groups, and which is of no less great practical consequence, concerns the fact that the species which we must regard as more or less close relatives on the ground of their general organisation bear in the structure of the organs of copulation (inclusive of the modified eighth segment of the *female*) a greater resemblance to one another than to the species which stand further away in the system. Representative species, such as *P. aristeus* and *rhesus*: *aegeus*, *tydeus*, *gambrisius*, *inopinatus*; *euchenor* and *depilis*, etc., have the organs in question built up after exactly the same plan, and the differences exhibited by these representative species in the organs of copulation are often not only far less obvious than the external differences of the species, but are sometimes so slight that the degree of divergence between two species is less than the degree of divergency between the extreme individuals of one of the two species; we refer for illustration to the figures given of the harpes of *P. aegeus* and *inopinatus*, *polytes* and *ambrax*. In less closely related species the similarity in the sexual armature is not so great as in those representative species which are phylogenetically younger forms; the organs are more divergently developed, and the peculiar modification of one or the other part of the apparatus often obscures the actual homology, so that the organs superficially compared are very dissimilar in appearance. Nevertheless a comparative study at once shows that the superficially dissimilar apparatus are developments of the same type. In *P. sarpedon* and *cloanthus* the close relationship of the valves and harpes (f. 96 and 149) is obvious. In *aristeus* (with *rhesus*, f. 72 to 82) the organs are more strongly modified, but the homology of the single parts with those of *P. cloanthus* is not difficult to perceive: *antiphates* has the organs again similar to those of *aristeus*, and the externally very dissimilar *P. delesserti*, *leucothoë*, and *xenocles* resemble *aristeus* in the structure of the *male* organs to a surprising extent, the principal prehensile parts of the valve consisting in these species, as in *aristeus* and *antiphates*, of a ventral dentate ridge, a subdorsal process, and the dorsal lobe of the bipartite valve, which parts respectively are homologous to *e*, *c*, *b* of f. 72 (*aristeus*). The vaginal armature agrees in this respect with the *male* armature; here again the most closely allied species have a greater similarity in the organs in question to one another than to less nearly related species: *P. ambrax* and *polytes* (f. 161 and 160); *P. aegeus*, *rumanzovius*, and *memnon* (f. 166, 170, and 171); *P. sarpedon*, *aristeus*, *agamemnon*, and *macfarlanei* (f. 182 to 187) illustrate this fact sufficiently. Although it would seem to follow from these statements that the degree of blood-relationship of two species to a third could easily be made out from the degree of similarity in the form of their organs of copulation, this inference of the facts would nevertheless be hasty and most probably erroneous, if we generalised the conclusion so as to apply to every species. Our researches convince us that it is true that in every group of closely allied species of *Papilio* the characters of the three independently variable organs, wing, harpe of *male*, and the vaginal armature of *female*, are such that each of these organs of every species is morphologically closer related to the respective organ of every other species of the group than to that of any species standing outside the group.

But within the group a species could very well be nearly related to another in the pattern of the wing, while it comes in the structure of the copulatory organs of the *male* or *female* closer to a third species, so that the relationship of the species *inter se* would appear to be different according as we take as the standard of arrangement the deviation in the one or the other organ.

If, however, it is true that the species which belong to the same group (of allied species) are in the genital armature more similar to one another than to the species of other groups, we have consequently to conclude that the organs of copulation are a safe guide to determine to which group a species belongs, which means that these organs can be made use of in generic classification. The great help which the genital armature affords to the systematist is beautifully illustrated by those species which bear to each other a superficial resemblance in pattern, such as *P. clytia* and *leucothoë* or *macareus*, *P. rhesus* and *philolaus*, which on the ground of the alleged relationship in pattern have been considered allied species. Though a careful examination of the wing-markings soon convinces us that we have here and in many other Papilios to do with an analogous development in pattern, as in the case of mimetic forms, which does not indicate blood-relationship, the demonstration of the dissimilarity in the morphology of the organs of copulation of those superficially similar species will be a more convincing guide in which direction the actual relationship is to be sought for.

Having thus arrived at the two conclusions, firstly, that identity in the sexual armature means specific identity, and secondly, that close relationship in these organs points to generic identity, the question arises, whether there are in the organs of copulation of specifically distinct Papilios, as opposed to specifically non-distinct forms, characters which *a priori* could be recognised as being of specific value, and hence would enable us to draw up a general rule applying to every case by which specifically distinct forms could be distinguished from specifically identical forms. The occurrence of individual and geographical variation in the copulatory organs, the latter kind of variation always associated with an independent variation in the wing-markings, renders it alone highly improbable that a general distinction between specific and subspecific characters is possible. A comparison, however, of the degree of divergency between subspecies with the degree of divergency between closely allied species proves that the quantitative amount of divergency between specifically identical forms can be superior to the quantitative amount of divergency between allied species. *P. inopinatus* differs in the harpe (f. 12) not so much from certain examples of *P. aegeus* as some of the latter do from one another (f. 4, 5); the difference between the harpe of *P. polytes polytes* (f. 18) and *P. polytes alphenor* (f. 33) is greater than that between *P. polytes* and *P. ambrax* (f. 35, 37); the difference between *P. aristeus parmatus* and *P. aristeus anticrates* in the harpes (f. 73, 75, 81, 83) is not inferior to the difference between *P. aristeus anticrates* and *P. rhesus*, which latter is considered to be a species distinct from *aristeus* (f. 82, 84). If, however, there are such cases like these in which that difference which is the greater in quantity is the smaller in quality (in respect to specific distinctness or non-distinctness), it consequently follows that it is impossible to say *a priori* which degree of quantitative divergence in the organs of copulation is in all Papilios of specific value. Hence a peculiarity observed in the sexual armature of an individual can be an aberrational, a subspecific, or a specific peculiarity; which of the three it actually is, we can learn only from a careful weighing of all the evidence. We have said in the introduction that the evidence

But within the group a species could very well be nearly related to another in the pattern of the wing, while it comes in the structure of the copulatory organs of the *male* or *female* closer to a third species, so that the relationship of the species *inter se* would appear to be different according as we take as the standard of arrangement the deviation in the one or the other organ.

If, however, it is true that the species which belong to the same group (of allied species) are in the genital armature more similar to one another than to the species of other groups, we have consequently to conclude that the organs of copulation are a safe guide to determine to which group a species belongs, which means that these organs can be made use of in generic classification. The great help which the genital armature affords to the systematist is beautifully illustrated by those species which bear to each other a superficial resemblance in pattern, such as *P. clytia* and *leucothoë* or *macareus*, *P. rhesus* and *philolaus*, which on the ground of the alleged relationship in pattern have been considered allied species. Though a careful examination of the wing-markings soon convinces us that we have here and in many other Papilios to do with an analogous development in pattern, as in the case of mimetic forms, which does not indicate blood-relationship, the demonstration of the dissimilarity in the morphology of the organs of copulation of those superficially similar species will be a more convincing guide in which direction the actual relationship is to be sought for.

Having thus arrived at the two conclusions, firstly, that identity in the sexual armature means specific identity, and secondly, that close relationship in these organs points to generic identity, the question arises, whether there are in the organs of copulation of specifically distinct Papilios, as opposed to specifically non-distinct forms, characters which *a priori* could be recognised as being of specific value, and hence would enable us to draw up a general rule applying to every case by which specifically distinct forms could be distinguished from specifically identical forms. The occurrence of individual and geographical variation in the copulatory organs, the latter kind of variation always associated with an independent variation in the wing-markings, renders it alone highly improbable that a general distinction between specific and subspecific characters is possible. A comparison, however, of the degree of divergency between subspecies with the degree of divergency between closely allied species proves that the quantitative amount of divergency between specifically identical forms can be superior to the quantitative amount of divergency between allied species. *P. inopinatus* differs in the harpe (f. 12) not so much from certain examples of *P. aegeus* as some of the latter do from one another (f. 4, 5); the difference between the harpe of *P. polytes polytes* (f. 18) and *P. polytes alphenor* (f. 33) is greater than that between *P. polytes* and *P. ambrax* (f. 35, 37); the difference between *P. aristeus parmatus* and *P. aristeus anticrates* in the harpes (f. 73, 75, 81, 83) is not inferior to the difference between *P. aristeus anticrates* and *P. rhesus*, which latter is considered to be a species distinct from *aristeus* (f. 82, 84). If, however, there are such cases like these in which that difference which is the greater in quantity is the smaller in quality (in respect to specific distinctness or non-distinctness), it consequently follows that it is impossible to say *a priori* which degree of quantitative divergence in the organs of copulation is in all Papilios of specific value. Hence a peculiarity observed in the sexual armature of an individual can be an aberrational, a subspecific, or a specific peculiarity; which of the three it actually is, we can learn only from a careful weighing of all the evidence. We have said in the introduction that the evidence remains quite incomplete as long as we do not know the limits of variation of the forms in question ; as these limits, however, can be made out, to a certain degree of correctness, only by comparing many individuals, it becomes self-evident that the question whether a certain peculiar character found in the genital armature of an individual or a number of individuals indicates specific distinctness or not, can only be decided with a certain degree of correctness when the variation of the sexual armature of the allied forms is known, *i.e.* after the examination of a great material.

When we said above that the degree of relationship between a number of closely allied forms could very well appear different according as we take the sexual armature or the wing-pattern as a guide in the arrangement of the forms, we did not give illustrations, because we had to recur to the phenomenon. If it really is true that there are cases in which two forms are in colour and markings the most closely related, while the structure of the genital armature stands in opposition to this relationship, pointing in quite a different direction, a comparison of the characters of the wings and the characters of the apparatus of copulation of the most closely allied forms, which are always geographical representative forms, with the aim of deducing the different relationship as indicated by similarities in the one or in the other organ, must throw a highly interesting light upon those questions which relate to the probable history of the geographical distribution and the origin of those forms.

B. PHENOMENA IN THE VARIATION OF THE ORGANS OF COPULATION RELATING TO SOME QUESTIONS OF THE GEOGRAPHICAL DISTRIBUTION OF ANIMALS.

When we speak here of representative forms, we do so regardless of their being specifically distinct from one another or not ; whether a geographical representative has reached the degree of divergent development which we call specific, or is still a subspecies, is of no importance for the following discussion ; the important point is, that there are differences between the representative forms.

Now, when we see that some Indian and Australian representatives are very similar in colour to one another and dissimilar to the forms inhabiting the interjacent countries, does that mean that the Indian and the Australian forms have separated after the more dissimilar representatives had branched off? When we find the Celebensian mountain form of *P. sarpedon* to bear a much greater resemblance in colour to the form inhabiting the Sunda Islands than to the form found on Celebes at lower elevations, is it correct to conclude that the Celebensian mountain form is a descendant of the Sunda Island form and indicates that there was at a former period a closer connection between Celebes and the Sunda Islands? When we observe in a great number of cases that the Javanese forms are similar to those from Malacca, while the forms from Sumatra and Borneo again are similar to one another, have we to infer from this fact that there was at one time a land-connection between Malacca and Java independent of Sumatra and Borneo? When West Africa and Madagascar are inhabited by two representatives with a narrow and interrupted band, while the East African form has a broad and uninterrupted band, can we conclude that the Madagascar form is the ancestor (or descendant) of the West African form? When, finally, we find Central America, the Greater Antilles, the Lesser Antilles, and Venezuela inhabited each by a representative bird or Papilio, and notice that in colour the forms from the first and third and the forms from the second and fourth localities are respectively similar, are we justified in so interpreting the fact as to say the Lesser Antilles have received the bird or insect from remains quite incomplete as long as we do not know the limits of variation of the forms in question ; as these limits, however, can be made out, to a certain degree of correctness, only by comparing many individuals, it becomes self-evident that the question whether a certain peculiar character found in the genital armature of an individual or a number of individuals indicates specific distinctness or not, can only be decided with a certain degree of correctness when the variation of the sexual armature of the allied forms is known, *i.e.* after the examination of a great material.

When we said above that the degree of relationship between a number of closely allied forms could very well appear different according as we take the sexual armature or the wing-pattern as a guide in the arrangement of the forms, we did not give illustrations, because we had to recur to the phenomenon. If it really is true that there are cases in which two forms are in colour and markings the most closely related, while the structure of the genital armature stands in opposition to this relationship, pointing in quite a different direction, a comparison of the characters of the wings and the characters of the apparatus of copulation of the most closely allied forms, which are always geographical representative forms, with the aim of deducing the different relationship as indicated by similarities in the one or in the other organ, must throw a highly interesting light upon those questions which relate to the probable history of the geographical distribution and the origin of those forms.

B. PHENOMENA IN THE VARIATION OF THE ORGANS OF COPULATION RELATING TO SOME QUESTIONS OF THE GEOGRAPHICAL DISTRIBUTION OF ANIMALS.

When we speak here of representative forms, we do so regardless of their being specifically distinct from one another or not ; whether a geographical representative has reached the degree of divergent development which we call specific, or is still a subspecies, is of no importance for the following discussion ; the important point is, that there are differences between the representative forms.

Now, when we see that some Indian and Australian representatives are very similar in colour to one another and dissimilar to the forms inhabiting the interjacent countries, does that mean that the Indian and the Australian forms have separated after the more dissimilar representatives had branched off? When we find the Celebensian mountain form of *P. sarpedon* to bear a much greater resemblance in colour to the form inhabiting the Sunda Islands than to the form found on Celebes at lower elevations, is it correct to conclude that the Celebensian mountain form is a descendant of the Sunda Island form and indicates that there was at a former period a closer connection between Celebes and the Sunda Islands ? When we observe in a great number of cases that the Javanese forms are similar to those from Malacca, while the forms from Sumatra and Borneo again are similar to one another, have we to infer from this fact that there was at one time a land-connection between Malacca and Java independent of Sumatra and Borneo ? When West Africa and Madagascar are inhabited by two representatives with a narrow and interrupted band, while the East African form has a broad and uninterrupted band, can we conclude that the Madagascar form is the ancestor (or descendant) of the West African form ? When, finally, we find Central America, the Greater Antilles, the Lesser Antilles, and Venezuela inhabited each by a representative bird or Papilio, and notice that in colour the forms from the first and third and the forms from the second and fourth localities are respectively similar, are we justified in so interpreting the fact as to say the Lesser Antilles have received the bird or insect from

Central America, while the form of the Greater Antilles is an immigrant from Venezuela? We are not going to deny that in a given case applying to one or the other of those questions an affirmative answer could be in accordance with the actual history of the origin of the respective form; but we shall endeavour to explain that similarities between representative forms are capable of being explained otherwise, and that there are many cases in which the agreement of two forms in respect to a certain character *must* be explained otherwise. Let us then inquire into the facts brought to light by our researches on the Eastern Papilios. As in the body of this paper the facts we have to refer to have been more fully dealt with, it will suffice to mention them here briefly without going in for a description of the organs concerned.

Papilio alcinous alcinous from Japan is represented on the Loo Choo Islands by *P. alcinous loochooanus* and in China by *P. alcinous confusus*. There are two prominent characters by which the forms are distinguished: *alcinous* has a black head and a dentate harpe, *loochooanus* a red head and a dentate harpe, and *confusus* a red head and a non-dentate harpe. In the colour of the head, therefore, *loochooanus* agrees with *confusus*, while in the harpe it agrees with *alcinous*; hence the relationship deducible from the similarity in colour of the head is directly opposed to the relationship indicated by the harpe, and it would be equally incorrect to say that *loochooanus* is a descendant of *confusus* on account of the similarity in colour, or to conclude that it has descended from *alcinous* because the harpes are the same; there would be just as much probability of correctness, if we consider only the naked facts here adduced, in the assumption that *alcinous* is the offspring of *loochooanus*, which itself descended from *confusus*, or that the reverse expresses the phylogenetic connection between the three forms, or that the three localities were inhabited at a former period by one form which later on became differentiated into the present three Papilios.

Papilio bathycles chiron from Sikkim, Assam, and Burma, and *P. bathycles bathycloides* from Malacca, Sumatra, and Borneo, are not always distinguishable in pattern, there occurring often specimens which, according to the wing-markings, could be regarded as belonging either to the one or to the other subspecies.

The Javanese representative *P. bathycles bathycles* stands in pattern not so close to *bathycloides* as this does to *chiron*. In the harpes *bathycloides* and *bathycles* come very near each other, while *chiron* exhibits a conspicuous difference from both in the development of the dorsal process (f. 46 to 50). Here again the form inhabiting the interjacent districts is more similar in the *male* copulatory organs to the one, in colour to the other representative.

The three subspecies of *P. cloanthus* inhabiting respectively China (*clymenus*), North India and Burma (*cloanthus*), and Sumatra (*sumatranus*), when arranged according to the similarity in pattern, would stand thus: *clymenus—cloanthus—sumatranus*, whereas in an arrangement according to the development of the harpe *cloanthus* would come first: *cloanthus—clymenus—sumatranus*.

The numerous subspecies of *P. sarpedon* provide us with a number of interesting facts. The Papuan form *choredon* of *sarpedon* inhabiting Australia and New Guinea (inclusive of the islands near it) bears in colour and pattern a rather close resemblance to the specimens of the spring brood of *sarpedon sarpedon* from North India, but is distinguished from the Indian form in the shape of the valve and harpe, in which organs *choredon* is similar to *anthedon* from the Southern Moluccas. The latter, however, differs in colour from *choredon*, agreeing in that

Central America, while the form of the Greater Antilles is an immigrant from Venezuela? We are not going to deny that in a given case applying to one or the other of those questions an affirmative answer could be in accordance with the actual history of the origin of the respective form: but we shall endeavour to explain that similarities between representative forms are capable of being explained otherwise, and that there are many cases in which the agreement of two forms in respect to a certain character *must* be explained otherwise. Let us then inquire into the facts brought to light by our researches on the Eastern Papilios. As in the body of this paper the facts we have to refer to have been more fully dealt with, it will suffice to mention them here briefly without going in for a description of the organs concerned.

Papilio alcinous alcinous from Japan is represented on the Loo Choo Islands by *P. alcinous loochooanus* and in China by *P. alcinous confusus*. There are two prominent characters by which the forms are distinguished: *alcinous* has a black head and a dentate harpe, *loochooanus* a red head and a dentate harpe, and *confusus* a red head and a non-dentate harpe. In the colour of the head, therefore, *loochooanus* agrees with *confusus*, while in the harpe it agrees with *alcinous*; hence the relationship deducible from the similarity in colour of the head is directly opposed to the relationship indicated by the harpe, and it would be equally incorrect to say that *loochooanus* is a descendant of *confusus* on account of the similarity in colour, or to conclude that it has descended from *alcinous* because the harpes are the same; there would be just as much probability of correctness, if we consider only the naked facts here adduced, in the assumption that *alcinous* is the offspring of *loochooanus*, which itself descended from *confusus*, or that the reverse expresses the phylogenetic connection between the three forms, or that the three localities were inhabited at a former period by one form which later on became differentiated into the present three Papilios.

Papilio bathycles chiron from Sikkim, Assam, and Burma, and *P. bathycles bathycloides* from Malacca, Sumatra, and Borneo, are not always distinguishable in pattern, there occurring often specimens which, according to the wing-markings, could be regarded as belonging either to the one or to the other subspecies.

The Javanese representative *P. bathycles bathycles* stands in pattern not so close to *bathycloides* as this does to *chiron*. In the harpes *bathycloides* and *bathycles* come very near each other, while *chiron* exhibits a conspicuous difference from both in the development of the dorsal process (f. 46 to 50). Here again the form inhabiting the interjacent districts is more similar in the *male* copulatory organs to the one, in colour to the other representative.

The three subspecies of *P. cloanthus* inhabiting respectively China (*clymenus*), North India and Burma (*cloanthus*), and Sumatra (*sumatranus*), when arranged according to the similarity in pattern, would stand thus: *clymenus—cloanthus—sumatranus*, whereas in an arrangement according to the development of the harpe *cloanthus* would come first: *cloanthus—clymenus—sumatranus*.

The numerous subspecies of *P. sarpedon* provide us with a number of interesting facts. The Papuan form *choredon* of *sarpedon* inhabiting Australia and New Guinea (inclusive of the islands near it) bears in colour and pattern a rather close resemblance to the specimens of the spring brood of *sarpedon sarpedon* from North India, but is distinguished from the Indian form in the shape of the valve and harpe, in which organs *choredon* is similar to *anthedon* from the Southern Moluccas. The latter, however, differs in colour from *choredon*, agreeing in that respect with *dodingensis* from the Northern Moluccas, which again has the harpe and valve different from those of *anthedon*, and is moreover distinguished from its colour-ally by the presence of an additional red spot on the underside of the hindwing. This spot is present only in *dodingensis* and the two Celebensian forms, *milon* found at lower elevations, and *monticolus* discovered recently at higher elevations on Mount Bonthain. The mountain form *monticolus* agrees in colour with *sarpedon sarpedon* from India and the Sunda Islands, also with the three representatives from the lesser Sunda Islands, comes in the shape of the band of the forewing near *dodingensis*, agrees in the size of the third spot with *timorensis*, stands in the *male* genital armature intermediate between *milon* and *dodingensis*, and hence differs in this respect obviously from *sarpedon*, has the before-mentioned red spot like *milon* and *dodingensis*, and differs from *milon* conspicuously in the shape of the wings, in which it agrees with *sarpedon* from the greater Sunda Islands. Would it really be possible to infer from such characters which contradict each other, pointing each in a certain direction of its own, the history of the origin of *choredon*, *dodingensis*, *monticolus*, etc.? Does not such a mixture of relations in opposite directions rather indicate that the similarities and dissimilarities found in representative forms are no signs of a closer or less close phylogenetic connection, and that we have to search for another explanation of the phenomena which will meet the contradiction of the characters?

Papilio aristeus anticrates from North India resembles the Queenslandian representative *parmatus* so much in pattern that Professor Eimer in his somewhat superficial work on the Papilios allied to *podalirius* ("Schwalbenschwänze") did not perceive the slight differences; whereas in the development of the valve and harpe *anticrates* and *parmatus* are opposite extremes. The forms inhabiting the interjacent countries are all much darker, and therefore have a closer resemblance to each other than to *anticrates* and *parmatus* (apart from some intergraduate examples). Hence the forms geographically widest apart would, according to the colour, be the nearest "related." The valve and harpe, however, are in *parmatus* exactly as in the externally different *aristeus* from the Moluccas, which again could be interpreted as being an expression of close relationship. In *hermocrates* from Burma, Borneo, the Philippine Islands, and the lesser Sunda Islands, the genital armature stands somewhat intermediate between that of *anticrates* and *parmatus*, but agrees in the form of the ventral dentate ridge obviously better with that of the first. As *hermocrates* and *aristeus* are connected by intergradations (occurring in Burma) in the wing-pattern as well as in the genital armature, an arrangement of the four allied forms according to the similarity in pattern would be thus: *parmatus* (Queensland and New Guinea)—*anticrates* (India)—*hermocrates* (Borneo, Philippines, lesser Sunda Islands)—*aristeus* (Moluccas); while the arrangement according to the similarity in the organs of copulation would be this: *anticrates*—*hermocrates*—*aristeus*—*parmatus*.

The representative occurring on the island of Celebes (and some islands south of it) is treated as a distinct species (by Eimer even as belonging to a widely different group). In the wing-markings it agrees best with *hermocrates*, but has mostly one band less; in the forewings being falcate it comes again closer to *hermocrates*, which is also geographically the nearest form, than to *aristeus*, *anticrates*, or *parmatus*. As *rhesus* is an exaggerated development of *P. aristeus*, differing from it in a similar way as *androcles* (Celebes) does from *antiphates* (India and Malayan Islands, Philippines, Moluccas), it sounds very reasonable to consider respect with *dodingensis* from the Northern Moluccas, which again has the harpe and valve different from those of *anthedon*, and is moreover distinguished from its colour-ally by the presence of an additional red spot on the underside of the hindwing. This spot is present only in *dodingensis* and the two Celebensian forms, *milon* found at lower elevations, and *monticolus* discovered recently at higher elevations on Mount Bonthain. The mountain form *monticolus* agrees in colour with *sarpedon sarpedon* from India and the Sunda Islands, also with the three representatives from the lesser Sunda Islands, comes in the shape of the band of the forewing near *dodingensis*, agrees in the size of the third spot with *timorensis*, stands in the *male* genital armature intermediate between *milon* and *dodingensis*, and hence differs in this respect obviously from *sarpedon*, has the before-mentioned red spot like *milon* and *dodingensis*, and differs from *milon* conspicuously in the shape of the wings, in which it agrees with *sarpedon* from the greater Sunda Islands. Would it really be possible to infer from such characters which contradict each other, pointing each in a certain direction of its own, the history of the origin of *choredon*, *dodingensis*, *monticolus*, etc.? Does not such a mixture of relations in opposite directions rather indicate that the similarities and dissimilarities found in representative forms are no signs of a closer or less close phylogenetic connection, and that we have to search for another explanation of the phenomena which will meet the contradiction of the characters?

Papilio aristeus anticrates from North India resembles the Queenslandian representative *parmatus* so much in pattern that Professor Eimer in his somewhat superficial work on the Papilios allied to *podalirius* ("Schwalbenschwänze") did not perceive the slight differences; whereas in the development of the valve and harpe *anticrates* and *parmatus* are opposite extremes. The forms inhabiting the interjacent countries are all much darker, and therefore have a closer resemblance to each other than to *anticrates* and *parmatus* (apart from some intergraduate examples). Hence the forms geographically widest apart would, according to the colour, be the nearest "related." The valve and harpe, however, are in *parmatus* exactly as in the externally different *aristeus* from the Moluccas, which again could be interpreted as being an expression of close relationship. In *hermocrates* from Burma, Borneo, the Philippine Islands, and the lesser Sunda Islands, the genital armature stands somewhat intermediate between that of *anticrates* and *parmatus*, but agrees in the form of the ventral dentate ridge obviously better with that of the first. As *hermocrates* and *aristeus* are connected by intergradations (occurring in Burma) in the wing-pattern as well as in the genital armature, an arrangement of the four allied forms according to the similarity in pattern would be thus: *parmatus* (Queensland and New Guinea)—*anticrates* (India)—*hermocrates* (Borneo, Philippines, lesser Sunda Islands)—*aristeus* (Moluccas); while the arrangement according to the similarity in the organs of copulation would be this: *anticrates*—*hermocrates*—*aristeus*—*parmatus*.

The representative occurring on the island of Celebes (and some islands south of it) is treated as a distinct species (by Eimer even as belonging to a widely different group). In the wing-markings it agrees best with *hermocrates*, but has mostly one band less; in the forewings being falcate it comes again closer to *hermocrates*, which is also geographically the nearest form, than to *aristeus*, *anticrates*, or *parmatus*. As *rhesus* is an exaggerated development of *P. aristeus*, differing from it in a similar way as *androcles* (Celebes) does from *antiphates* (India and Malayan Islands, Philippines, Moluccas), it sounds very reasonable to consider it to have developed from that form of *P. aristeus* to which it comes nearest in the before-mentioned points, namely from *P. aristeus hermocrates*. An examination of the valve of the *male* shows, however, that there is also very good reason to deduce *rhesus* from *P. aristeus aristeus* or *parmatus*. The ventral dentate ridge is in the eastern forms (*rhesus*, *aristeus*, *parmatus*) half-ring-shaped (f. 83, 84), and at a glance distinguishable from the smaller, only slightly curved, ridge of the western forms (*anticrates* and *hermocrates*, f. 73, 74); as intergradations in the two kinds of ridge are unknown (although we have examined a great many individuals), the constant difference in the ridge would be regarded by many systematists as justifying a specific separation of the western forms from the eastern ones, in which case *P. rhesus* agreeing in the ridge very well with the eastern forms, apart from minor differences, would appear to be closer allied to *aristeus* and *parmatus* than to *hermocrates* and *anticrates*, and hence could be considered a descendant of *P. aristeus aristeus* from the Moluccas.

If we take A, B, C as three geographical representatives, a_1 and a_2 as the different degrees of development of the wings of these forms, and b_1 and b_2 as the different degrees of development of the organs of copulation, the several cases above adduced, which we think sufficiently illustrate the questions we are to deal with, can be put diagrammatically as follows:—

A	B	C
a_1	a_1	a_2
b_1	b_2	b_2

The dilemma arising from the contradiction of the characters of geographical representatives allows a satisfactory solution, if we take into account, firstly, that according to the theory of evolution the peculiar modifications of the organs of a certain animal are partly inherited and partly acquired, and that therefore a similarity between two forms, and a dissimilarity, *a priori* neither prove nor disprove a close phylogenetic connection of the forms; and secondly, that when the similarity between two forms is due to inheritance the character common to the two forms is inherited either by both independently from the common ancestor, from which also other forms which have lost that character have descended, or by one of the two forms from the other. The conclusions generally deduced in systematic and other works from the similarity and dissimilarity of geographical representatives in respect to the Geographical Distribution of Animals as a science (not as a mere statement of facts) are to our mind mostly based on the erroneous assumptions, firstly, that every similarity is due to inheritance, and secondly, that the presence of a peculiarity in two forms must necessarily be due to the common character being inherited by one of the two forms from the other. Let us, then, briefly inquire into the question of the probable origin of the similarities and dissimilarities of allied forms, and try to arrive at a correct estimate of their actual value in our judgment of the relationship of the forms in which they are observed.

If we recall to mind that the development of a species into more species is possible only by means of isolated transforming factors associated with a more or less complete prevention of the affected portion of the species from interbreeding with the original stock, the distinguishing characters of locally separated allied forms, which we must regard as the outcome of the transformation of a common ancestral form, must be due to the effect of isolated evolutionistic factors of any kind present in the district inhabited by each single representative form. It is quite possible that when a species separates thus, first into subspecies and then into it to have developed from that form of *P. aristeus* to which it comes nearest in the before-mentioned points, namely from *P. aristeus hermocrates.* An examination of the valve of the *male* shows, however, that there is also very good reason to deduce *rhesus* from *P. aristeus aristeus* or *parmatus.* The ventral dentate ridge is in the eastern forms (*rhesus*, *aristeus*, *parmatus*) half-ring-shaped (f. 83, 84), and at a glance distinguishable from the smaller, only slightly curved, ridge of the western forms (*anticrates* and *hermocrates*, f. 73, 74); as intergradations in the two kinds of ridge are unknown (although we have examined a great many individuals), the constant difference in the ridge would be regarded by many systematists as justifying a specific separation of the western forms from the eastern ones, in which case *P. rhesus* agreeing in the ridge very well with the eastern forms, apart from minor differences, would appear to be closer allied to *aristeus* and *parmatus* than to *hermocrates* and *anticrates*, and hence could be considered a descendant of *P. aristeus aristeus* from the Moluccas.

If we take A, B, C as three geographical representatives, a_1 and a_2 as the different degrees of development of the wings of these forms, and b_1 and b_2 as the different degrees of development of the organs of copulation, the several cases above adduced, which we think sufficiently illustrate the questions we are to deal with, can be put diagrammatically as follows:—

A	B	C
a_1	a_1	a_2
b_1	b_2	b_2

The dilemma arising from the contradiction of the characters of geographical representatives allows a satisfactory solution, if we take into account, firstly, that according to the theory of evolution the peculiar modifications of the organs of a certain animal are partly inherited and partly acquired, and that therefore a similarity between two forms, and a dissimilarity, *a priori* neither prove nor disprove a close phylogenetic connection of the forms; and secondly, that when the similarity between two forms is due to inheritance the character common to the two forms is inherited either by both independently from the common ancestor, from which also other forms which have lost that character have descended, or by one of the two forms from the other. The conclusions generally deduced in systematic and other works from the similarity and dissimilarity of geographical representatives in respect to the Geographical Distribution of Animals as a science (not as a mere statement of facts) are to our mind mostly based on the erroneous assumptions, firstly, that every similarity is due to inheritance, and secondly, that the presence of a peculiarity in two forms must necessarily be due to the common character being inherited by one of the two forms from the other. Let us, then, briefly inquire into the question of the probable origin of the similarities and dissimilarities of allied forms, and try to arrive at a correct estimate of their actual value in our judgment of the relationship of the forms in which they are observed.

If we recall to mind that the development of a species into more species is possible only by means of isolated transforming factors associated with a more or less complete prevention of the affected portion of the species from interbreeding with the original stock, the distinguishing characters of locally separated allied forms, which we must regard as the outcome of the transformation of a common ancestral form, must be due to the effect of isolated evolutionistic factors of any kind present in the district inhabited by each single representative form. It is quite possible that when a species separates thus, first into subspecies and then into representative species, one of the descendant forms remains identical with the original form; but considering that in all widely distributed groups of representative forms a considerable time must have elapsed before the insects could spread over the whole area—for instance, from North-West India to the Solomon Islands—it is at least in such cases more probable that the form now inhabiting the country where the ancestral form lived has also more or less changed in characters. And this is the more likely to be true as we know from experiments that the time required to bring about a change in colour in *Lepidoptera* is very short, and as we further know that a change, within a short time, has taken place in the famous Porto Santo rabbits, some birds, and a great number of plants. From the comparison of seasonal forms, which are the more different the greater the contrast of the seasons is, with artificially produced varieties, we can with safety conclude that the degree of divergency of representative forms largely (not entirely) depends on the intensity of the transmuting factors, and that therefore a wider gap between two otherwise allied forms does not necessarily imply that the two animals or plants have been separated for a longer time than less different allies. As it is also well known that the intensity of the biological factors does not gradually increase or decrease as we proceed from one (geographical) extremity of the range of a group of representative forms to the other extremity, it is evident that the degree of diversity of two forms can be independent of the geographical position of the areas inhabited, and that the more similar forms can live widely apart, while the more dissimilar forms may live closer together.

Though the differences between representative forms are the effect of the action of some kind of local biological factors, it does not follow with necessity that the respective factors are found in every place where a certain form now occurs; on the contrary, we have instances that species when living under different conditions do not show any change in their characters. For example, the island of Kalao, south of Celebes, is inhabited by the Celebensian *Papilio rhesus*, and the Kalao individuals are to our knowledge not distinguishable from the Celebes *rhesus*. The other species of *Papilio* found on Kalao (and Djampea, which is close by) are all conspicuously different from the Celebensian representatives, and have mostly developed to peculiar forms not known (as such) from anywhere else; hence there must be biological factors peculiar to those islands which have not had any effect on *P. rhesus*. That *rhesus* is a true Celebensian insect (*i.e.* originated from the ancestor of *P. aristeus* on Celebes) is virtually proved by its characters being quite analogous to those of many other Celebensian forms. Curiously enough, on the island of Djampea, which lies north of Kalao and therefore is somewhat closer to Celebes, Mr. A. Everett obtained no specimens of *rhesus*, but a long series of the Malayan representative *P. aristeus hermocrates*, during the same month when he found a good series of individuals of *P. rhesus* and no *hermocrates* on Kalao. The fact that *rhesus* is the same on Celebes and Kalao admits three explanations: (1) The biological (transmuting) factors are in respect to *rhesus* the same on both islands, which would mean that on Djampea, as inhabited by a representative, the corresponding factors must be different. (2) The biological factors are different on Celebes and Kalao, but the characters acquired by *rhesus* under the action of the Celebensian factors have become inheritable. (3) The characters of *rhesus* and its representatives are not acquired under the influence of biological factors.

If, however, a change in the biological factors does not necessarily imply that a change in the characters of every living being will take place, it is intelligible representative species, one of the descendant forms remains identical with the original form; but considering that in all widely distributed groups of representative forms a considerable time must have elapsed before the insects could spread over the whole area—for instance, from North-West India to the Solomon Islands—it is at least in such cases more probable that the form now inhabiting the country where the ancestral form lived has also more or less changed in characters. And this is the more likely to be true as we know from experiments that the time required to bring about a change in colour in *Lepidoptera* is very short, and as we further know that a change, within a short time, has taken place in the famous Porto Santo rabbits, some birds, and a great number of plants. From the comparison of seasonal forms, which are the more different the greater the contrast of the seasons is, with artificially produced varieties, we can with safety conclude that the degree of divergency of representative forms largely (not entirely) depends on the intensity of the transmuting factors, and that therefore a wider gap between two otherwise allied forms does not necessarily imply that the two animals or plants have been separated for a longer time than less different allies. As it is also well known that the intensity of the biological factors does not gradually increase or decrease as we proceed from one (geographical) extremity of the range of a group of representative forms to the other extremity, it is evident that the degree of diversity of two forms can be independent of the geographical position of the areas inhabited, and that the more similar forms can live widely apart, while the more dissimilar forms may live closer together.

Though the differences between representative forms are the effect of the action of some kind of local biological factors, it does not follow with necessity that the respective factors are found in every place where a certain form now occurs; on the contrary, we have instances that species when living under different conditions do not show any change in their characters. For example, the island of Kalao, south of Celebes, is inhabited by the Celebensian *Papilio rhesus*, and the Kalao individuals are to our knowledge not distinguishable from the Celebes *rhesus*. The other species of *Papilio* found on Kalao (and Djampea, which is close by) are all conspicuously different from the Celebensian representatives, and have mostly developed to peculiar forms not known (as such) from anywhere else; hence there must be biological factors peculiar to those islands which have not had any effect on *P. rhesus*. That *rhesus* is a true Celebensian insect (*i.e.* originated from the ancestor of *P. aristeus* on Celebes) is virtually proved by its characters being quite analogous to those of many other Celebensian forms. Curiously enough, on the island of Djampea, which lies north of Kalao and therefore is somewhat closer to Celebes, Mr. A. Everett obtained no specimens of *rhesus*, but a long series of the Malayan representative *P. aristeus hermocrates*, during the same month when he found a good series of individuals of *P. rhesus* and no *hermocrates* on Kalao. The fact that *rhesus* is the same on Celebes and Kalao admits three explanations: (1) The biological (transmuting) factors are in respect to *rhesus* the same on both islands, which would mean that on Djampea, as inhabited by a representative, the corresponding factors must be different. (2) The biological factors are different on Celebes and Kalao, but the characters acquired by *rhesus* under the action of the Celebensian factors have become inheritable. (3) The characters of *rhesus* and its representatives are not acquired under the influence of biological factors.

If, however, a change in the biological factors does not necessarily imply that a change in the characters of every living being will take place, it is intelligible that in geographical representatives, which live under the influence of different biological factors, one or the other character can remain unaffected. When this takes place independently in several forms which represent each other, the preserved character of the common ancestor renders those forms more similar to each other than to the other representatives which live under conditions that have modified the respective character, while the actual blood-relationship is the same between all the forms. On the other hand, it could also be thought possible that, when a species gradually spreads over a larger area and develops into a number of representative forms, now and again a character acquired by a new form *A* occurring in locality *M* will remain unaltered in form *B* living in locality *N* which is a descendant of *A*; in this case the presence of the same character in forms *A* and *B* would imply that the forms are closer connected with one another than *B* is with any other ally except its own descendants. However, if we admit this case to occur, we should maintain that an acquired character is inheritable when the conditions which have brought it into appearance are absent, and we thus should decide offhand the much-contested question whether acquired characters are or are not inheritable. Notwithstanding we believe that ultimately the inheritance of acquired characters will be proved, the contest clearly shows that it is in every case a mere assumption, if we conclude from the presence of the same character or similar characters in two representative forms that one of the two is the parent, the other the daughter form.

If divergency is the effect of transmuting factors, could not similarity also be the outcome of biological factors in different districts? Many facts, for instance the similarity of desert forms, point to an affirmative answer; but we have an almost certain proof furnished us by the experiments* of Standfuss, who succeeded in breeding under artificial conditions from ordinary European *Lepidoptera* such forms as come close to their geographical representatives. As Standfuss was able to produce from our common *Vanessa antiopa* specimens similar to the Central American form (*thomsoni*), there can no longer be any doubt that a similarity in a character of the representative forms of a species can come about in widely separated countries, and will come about when the conditions are favourable.

Taking into account all the points here adduced, it seems to us obvious that all the evidence points to one end, namely, that the similarities and dissimilarities exhibited by representative forms are not an expression of closer or less close phylogenetic connection, but an expression of the similar or dissimilar effect of the action of the different and similar biological factors on the organs in every locality. If we apply this conclusion, which is a necessary consequence of the assumption that the theory of evolution is correct, to the facts observed in the Papilios, there is no longer any contradiction in the characters of the wing and the characters of the organs of copulation. That *Papilio aristeus anticrates* from India agrees with the Papuan representative in the colour, but disagrees with it entirely in the harpe, that the Chinese *P. cloanthus* is in the harpe more similar to the Sumatran than to the North Indian form, that *P. sarpedon teredon* from Ceylon and South India agrees best in the wings and genital armature with the forms occurring on the lesser Sunda Islands and disagrees widely with the form inhabiting all the interjacent countries, that the Nicobar form of *P. agamemnon* is in the presence of a series of red spots on the underside of the hindwing similar to the representative from the that in geographical representatives, which live under the influence of different biological factors, one or the other character can remain unaffected. When this takes place independently in several forms which represent each other, the preserved character of the common ancestor renders those forms more similar to each other than to the other representatives which live under conditions that have modified the respective character, while the actual blood-relationship is the same between all the forms. On the other hand, it could also be thought possible that, when a species gradually spreads over a larger area and develops into a number of representative forms, now and again a character acquired by a new form *A* occurring in locality *M* will remain unaltered in form *B* living in locality *N* which is a descendant of *A*; in this case the presence of the same character in forms *A* and *B* would imply that the forms are closer connected with one another than *B* is with any other ally except its own descendants. However, if we admit this case to occur, we should maintain that an acquired character is inheritable when the conditions which have brought it into appearance are absent, and we thus should decide offhand the much-contested question whether acquired characters are or are not inheritable. Notwithstanding we believe that ultimately the inheritance of acquired characters will be proved, the contest clearly shows that it is in every case a mere assumption, if we conclude from the presence of the same character or similar characters in two representative forms that one of the two is the parent, the other the daughter form.

---

* Standfuss, *Handbuch für Schmetterlingssammler* 1896.

If divergency is the effect of transmuting factors, could not similarity also be the outcome of biological factors in different districts? Many facts, for instance the similarity of desert forms, point to an affirmative answer; but we have an almost certain proof furnished us by the experiments* of Standfuss, who succeeded in breeding under artificial conditions from ordinary European *Lepidoptera* such forms as come close to their geographical representatives. As Standfuss was able to produce from our common *Vanessa antiopa* specimens similar to the Central American form (*thomsoni*), there can no longer be any doubt that a similarity in a character of the representative forms of a species can come about in widely separated countries, and will come about when the conditions are favourable.

Taking into account all the points here adduced, it seems to us obvious that all the evidence points to one end, namely, that the similarities and dissimilarities exhibited by representative forms are not an expression of closer or less close phylogenetic connection, but an expression of the similar or dissimilar effect of the action of the different and similar biological factors on the organs in every locality. If we apply this conclusion, which is a necessary consequence of the assumption that the theory of evolution is correct, to the facts observed in the Papilios, there is no longer any contradiction in the characters of the wing and the characters of the organs of copulation. That *Papilio aristeus anticrates* from India agrees with the Papuan representative in the colour, but disagrees with it entirely in the harpe, that the Chinese *P. cloanthus* is in the harpe more similar to the Sumatran than to the North Indian form, that *P. sarpedon teredon* from Ceylon and South India agrees best in the wings and genital armature with the forms occurring on the lesser Sunda Islands and disagrees widely with the form inhabiting all the interjacent countries, that the Nicobar form of *P. agamemnon* is in the presence of a series of red spots on the underside of the hindwing similar to the representative from the

---

* Standfuss, *Handbuch für Schmetterlingssammler* 1896.

Solomon Islands (!), and so on, is no more miraculous than the fact that there *is* seasonal and local variation.

Now, when we observe, for instance, that the Chinese *P. eurypylus* agrees best with the Andaman form of that species, and that the Chinese *P. antiphates* comes close to the Ceylon form, while in both cases the representative inhabiting North India, Burma, and Tenasserim is different, it would certainly sound preposterous to explain the similarity in characters by assuming that there was at a former period a land-connection between Ceylon, the Andaman Islands, and China independent of Continental India. If we concede that this explanation cannot possibly be accepted, and that consequently the similarity finds a correct explanation in the assumption that it is merely the consequence of the similar effect of the biological factors—the effect is positive in respect to the characters which are modified, and negative in respect to the characters which are not modified—of Ceylon, the Andamans, and China, it is not difficult to perceive what great bearings the questions here discussed have on the Geographical Distribution of Animals. Before proceeding to draw the consequences, let us for a moment consider what is the aim of the study of the Distribution of Animals.

"If we keep in view . . . that the present distribution of animals upon the several parts of the earth's surface is the final product of . . . the wonderful revolutions in organic and inorganic nature," says Wallace,* . . . "it will be evident that the study of the distribution of animals and plants may add greatly to our knowledge of the past history of our globe. It may reveal to us, in a manner which no other evidence can, which are the oldest and most permanent features of the earth's surface, and which the newest. It may indicate the existence of islands or continents now sunk beneath the ocean, and which have left no record of their existence save the animal and vegetable productions which have migrated to adjacent lands. It thus becomes an important adjunct to geology. . . . Our present study may often enable us, not only to say where lands must have recently disappeared, but also to form some judgment as to their extent, and the time that has elapsed since their submersion." Indeed, the distribution of animals and plants, especially if the extinct forms are also taken into account, illustrates wonderfully the past history of the earth's surface, and the main object of the study of the distribution of animals and plants is to arrive at conclusions as to the probable past changes in the geological features of the earth. This has so plainly been recognised by nearly all recent systematists, as a glance in a volume of the *Proceedings of the Zoological Society* or of the *Ibis* will show, that, when dealing with a certain group of animals from a certain locality, they endeavour to draw from the affinities in the fauna of the respective district with that of other districts conclusions relating to the geological history of the locality, and it is very generally assumed that similarity in the components of the fauna of two areas means close geological connection, while great dissimilarity means long geological separation. So true this is in a great many cases, so erroneous is the generalisation. Nevertheless it has very often been entirely lost sight of that the present distribution of animals and plants is, to use Wallace's words, "the final product of revolutions in inorganic *and organic* nature," and that accordingly the differences in the fauna of neighbouring districts and the similarities in the fauna of geographically widely separate areas can be quite independent of the geological history of the region in question. If we now recall to mind what we have said above about the similarity

---

* *Distribution of Animals* 1876, p. 7.

Solomon Islands (!), and so on, is no more miraculous than the fact that there *is* seasonal and local variation.

Now, when we observe, for instance, that the Chinese *P. eurypylus* agrees best with the Andaman form of that species, and that the Chinese *P. antiphates* comes close to the Ceylon form, while in both cases the representative inhabiting North India, Burma, and Tenasserim is different, it would certainly sound preposterous to explain the similarity in characters by assuming that there was at a former period a land-connection between Ceylon, the Andaman Islands, and China independent of Continental India. If we concede that this explanation cannot possibly be accepted, and that consequently the similarity finds a correct explanation in the assumption that it is merely the consequence of the similar effect of the biological factors—the effect is positive in respect to the characters which are modified, and negative in respect to the characters which are not modified—of Ceylon, the Andamans, and China, it is not difficult to perceive what great bearings the questions here discussed have on the Geographical Distribution of Animals. Before proceeding to draw the consequences, let us for a moment consider what is the aim of the study of the Distribution of Animals.

"If we keep in view . . . that the present distribution of animals upon the several parts of the earth's surface is the final product of . . . the wonderful revolutions in organic and inorganic nature," says Wallace,* . . . "it will be evident that the study of the distribution of animals and plants may add greatly to our knowledge of the past history of our globe. It may reveal to us, in a manner which no other evidence can, which are the oldest and most permanent features of the earth's surface, and which the newest. It may indicate the existence of islands or continents now sunk beneath the ocean, and which have left no record of their existence save the animal and vegetable productions which have migrated to adjacent lands. It thus becomes an important adjunct to geology. . . . Our present study may often enable us, not only to say where lands must have recently disappeared, but also to form some judgment as to their extent, and the time that has elapsed since their submersion." Indeed, the distribution of animals and plants, especially if the extinct forms are also taken into account, illustrates wonderfully the past history of the earth's surface, and the main object of the study of the distribution of animals and plants is to arrive at conclusions as to the probable past changes in the geological features of the earth. This has so plainly been recognised by nearly all recent systematists, as a glance in a volume of the *Proceedings of the Zoological Society* or of the *Ibis* will show, that, when dealing with a certain group of animals from a certain locality, they endeavour to draw from the affinities in the fauna of the respective district with that of other districts conclusions relating to the geological history of the locality, and it is very generally assumed that similarity in the components of the fauna of two areas means close geological connection, while great dissimilarity means long geological separation. So true this is in a great many cases, so erroneous is the generalisation. Nevertheless it has very often been entirely lost sight of that the present distribution of animals and plants is, to use Wallace's words, "the final product of revolutions in inorganic *and organic* nature," and that accordingly the differences in the fauna of neighbouring districts and the similarities in the fauna of geographically widely separate areas can be quite independent of the geological history of the region in question. If we now recall to mind what we have said above about the similarity and dissimilarity in the characters of representative forms, it will be evident that the difference in the fauna of neighbouring districts is due to two kinds of entirely different factors, *geological* and *biological* factors, and that the study of the geographical distribution of animals and plants consists of two branches—the *geological branch*, which has to do with such discrepancies in the fauna and flora as allow conclusions to be drawn as to the geological transformation of the *districts* in question, and the *biological branch*, which has to do with those other differences from which we can draw conclusions as to the transformation of the *animals* and *plants* in question. And now we can extend our former conclusion that differences in the characters of representative forms which stand in close phylogenetic connection are an expression of the differences in the biological factors of the districts concerned, to those forms which are representatives in a biological sense and exclude each other in consequence of a similarity in habits, and again to those which cannot exist beside one another in the same district, because they are so different in habits that they require a respectively different environment. It is certainly conceivable that the absence of woodpeckers, which abound in the Indo-Malayan Region, from the lesser Sunda Islands (and all the islands farther east) could be due to the presence of cockatoos, which are, like those, hole-breeders, though we do not maintain that this similarity in habits is the actual reason of the two widely different groups of birds excluding each other in that region: while, again, the discrepancy in the composition of the West African from the East African fauna is readily explained by the former being a wet forest country, the latter an open and dry country, and the affinities which the West African forest region has in the fauna with the Indo-Malayan Region, and the analogous affinities of East Africa with Western India, are consequences of similar physiographical conditions of the countries, just as the difference in the characters of the West African, East African, and Malagassic morphologically allied representative forms—which I shall call *morphological* representatives, as distinctive of *biological* representatives—are due to differences in the transmuting factors of the respective districts. The contrast in which these explanations of faunistic discrepancies stand to the explanation of those discrepancies which are caused by geological factors is strikingly illustrated by a comparison of the fauna of Madagascar with that of Africa, in so far as we have rightly to conclude from the absence of the large *Carnivora* and *Ungulata*, so abundant in Africa, from Madagascar that this island must already have been isolated from Africa by a wide sea-arm at that time when those animals immigrated from the North into the Aethiopian Region.

---

* *Distribution of Animals* 1876, p. 7.

The difference in the fauna of various districts is further dependent on the fact that different animals are, as said before, affected by the transmuting factors of a certain locality in a different degree, so that often some forms are, while some are not, modified in characters. We have consequently to take into account also the physiological constitution of the animals when treating upon zoogeographical questions. Hence it is evident that the result of the division of the earth's surface in zoogeographical areas must be different according as we take the faunistic discrepancies depending on the geological factors as the base of division, or those differences which are caused by the biological factors; and again, if we take the biological division, it is obvious that the extent of the areas must be quite different according as to which animals are taken into consideration.

Although *Wallace* has emphasised, throughout his *Geographical Distribution of Animals*, the high importance of the geological branch of zoogeography relating to and dissimilarity in the characters of representative forms, it will be evident that the difference in the fauna of neighbouring districts is due to two kinds of entirely different factors, *geological* and *biological* factors, and that the study of the geographical distribution of animals and plants consists of two branches—the *geological branch*, which has to do with such discrepancies in the fauna and flora as allow conclusions to be drawn as to the geological transformation of the *districts* in question, and the *biological branch*, which has to do with those other differences from which we can draw conclusions as to the transformation of the *animals* and *plants* in question. And now we can extend our former conclusion that differences in the characters of representative forms which stand in close phylogenetic connection are an expression of the differences in the biological factors of the districts concerned, to those forms which are representatives in a biological sense and exclude each other in consequence of a similarity in habits, and again to those which cannot exist beside one another in the same district, because they are so different in habits that they require a respectively different environment. It is certainly conceivable that the absence of woodpeckers, which abound in the Indo-Malayan Region, from the lesser Sunda Islands (and all the islands farther east) could be due to the presence of cockatoos, which are, like those, hole-breeders, though we do not maintain that this similarity in habits is the actual reason of the two widely different groups of birds excluding each other in that region : while, again, the discrepancy in the composition of the West African from the East African fauna is readily explained by the former being a wet forest country, the latter an open and dry country, and the affinities which the West African forest region has in the fauna with the Indo-Malayan Region, and the analogous affinities of East Africa with Western India, are consequences of similar physiographical conditions of the countries, just as the difference in the characters of the West African, East African, and Malagassic morphologically allied representative forms—which I shall call *morphological* representatives, as distinctive of *biological* representatives—are due to differences in the transmuting factors of the respective districts. The contrast in which these explanations of faunistic discrepancies stand to the explanation of those discrepancies which are caused by geological factors is strikingly illustrated by a comparison of the fauna of Madagascar with that of Africa, in so far as we have rightly to conclude from the absence of the large *Carnivora* and *Ungulata*, so abundant in Africa, from Madagascar that this island must already have been isolated from Africa by a wide sea-arm at that time when those animals immigrated from the North into the Aethiopian Region.

The difference in the fauna of various districts is further dependent on the fact that different animals are, as said before, affected by the transmuting factors of a certain locality in a different degree, so that often some forms are, while some are not, modified in characters. We have consequently to take into account also the physiological constitution of the animals when treating upon zoogeographical questions. Hence it is evident that the result of the division of the earth's surface in zoogeographical areas must be different according as we take the faunistic discrepancies depending on the geological factors as the base of division, or those differences which are caused by the biological factors; and again, if we take the biological division, it is obvious that the extent of the areas must be quite different according as to which animals are taken into consideration.

Although *Wallace* has emphasised, throughout his *Geographical Distribution of Animals*, the high importance of the geological branch of zoogeography relating to the past history of the earth and its inhabitants, the minor zoogeographical districts have by most authors been delimitated according to differences which are the effect of biological factors. Considering, however, that different environment, such as forest, open land and desert, fresh and salt water, naturally gives subsistence to different animals, and that therefore physiographically different districts *a priori* are known to have a different fauna, the division of the earth's surface in such zoogeographical districts as are identical with physiographical districts (Sharpe's West African Subregion = district covered with forest; Merriam's Sonoran Subregion of North America = arid country) is as such of very little value, concerning more the geographer than the zoologist. And taking further into account that we now know perfectly well that in every district where the physiographical (and meteorological) conditions are different from those of other districts these differences are accompanied by modifications of the characters of some of the animals, the simple statement that a certain number of the inhabitants are different from the representative forms of the adjacent districts is, like the mere record of the discrepancy in the composition of the fauna, of little consequence for science, as from those statements as such no new general conclusions can be drawn. The biological branch of the study of the geographical distribution of animals, therefore, must have another aim, and that is to be to Zoology what the geological branch is to Geology, namely an adjunctive science which, by a comparative study of the differences in the environment and those in the animals, may help greatly to find the causal connection between the modifications in the organs of the animals and in the environment (in the widest sense), and thus could reveal to us the history of the descent of the forms of animals.

For the sake of illustration let us apply these conclusions to the *Papilio* fauna of a small area, for instance the lesser Sunda Islands. We select this group of islands for two reasons: firstly, because the discrepancy existing between their fauna and that of the larger Sunda Islands has been accounted for by Wallace by geological factors (*Wallace's line*); and secondly, because our conclusions derived from the Papilios stand in opposition to those which Wallace derived from the avifauna. As a complete exposition of the zoogeographical relations of the islands between Lombok and Timor * would be much too extensive for our present purpose, we will restrict the discussion chiefly to the two questions: (1) what conclusions can we draw from the composition of the *Papilio* fauna of the lesser Sunda Islands with respect to the geological history of the group of islands? and (2) is there anything in the distinguishing characters of the Papilios which can serve to solve a question relating to the phylogeny of animals?

The islands of Lombok, Sambawa, Sumba eastward as far as Letti and Moa, are inhabited by fifty odd different forms of *Papilio*, which we can arrange in eighteen series of closely allied representatives. Of these eighteen series one (*canopus*-series) is distributed farther east over the Tenimber Islands and North Australia to the New Hebrides, but has also some allies in the Indo-Malayan Region; the *peranthus*-series occurs from Java to New Guinea, but is absent from Australia; another, *haliphron*-series, is found in Celebes and not in the Indo-Malayan Region: a fourth, *antiphates*-series, is found all over the Indo-Malayan Region, Celebes, and the Northern Moluccas, but is absent from the Southern Moluccas, Australia, New Guinea, and the islands farther east. Seven series reappear in the Indo-Malayan the past history of the earth and its inhabitants, the minor zoogeographical districts have by most authors been delimitated according to differences which are the effect of biological factors. Considering, however, that different environment, such as forest, open land and desert, fresh and salt water, naturally gives subsistence to different animals, and that therefore physiographically different districts *a priori* are known to have a different fauna, the division of the earth's surface in such zoogeographical districts as are identical with physiographical districts (Sharpe's West African Subregion = district covered with forest; Merriam's Sonoran Subregion of North America = arid country) is as such of very little value, concerning more the geographer than the zoologist. And taking further into account that we now know perfectly well that in every district where the physiographical (and meteorological) conditions are different from those of other districts these differences are accompanied by modifications of the characters of some of the animals, the simple statement that a certain number of the inhabitants are different from the representative forms of the adjacent districts is, like the mere record of the discrepancy in the composition of the fauna, of little consequence for science, as from those statements as such no new general conclusions can be drawn. The biological branch of the study of the geographical distribution of animals, therefore, must have another aim, and that is to be to Zoology what the geological branch is to Geology, namely an adjunctive science which, by a comparative study of the differences in the environment and those in the animals, may help greatly to find the causal connection between the modifications in the organs of the animals and in the environment (in the widest sense), and thus could reveal to us the history of the descent of the forms of animals.

---

* Compare also Doherty, *The Butterflies of Sumba and Sambawa*, in *Journ. As. Soc. Beng.* 1891; Pagenstecher, *Ueber die Lepidopteren von Sumba und Sambawa*, in *Jahrb. Nass. Ver. Nat.* 1896.

For the sake of illustration let us apply these conclusions to the *Papilio* fauna of a small area, for instance the lesser Sunda Islands. We select this group of islands for two reasons: firstly, because the discrepancy existing between their fauna and that of the larger Sunda Islands has been accounted for by Wallace by geological factors (*Wallace's line*); and secondly, because our conclusions derived from the Papilios stand in opposition to those which Wallace derived from the avifauna. As a complete exposition of the zoogeographical relations of the islands between Lombok and Timor * would be much too extensive for our present purpose, we will restrict the discussion chiefly to the two questions: (1) what conclusions can we draw from the composition of the *Papilio* fauna of the lesser Sunda Islands with respect to the geological history of the group of islands? and (2) is there anything in the distinguishing characters of the Papilios which can serve to solve a question relating to the phylogeny of animals?

The islands of Lombok, Sambawa, Sumba eastward as far as Letti and Moa, are inhabited by fifty odd different forms of *Papilio*, which we can arrange in eighteen series of closely allied representatives. Of these eighteen series one (*canopus*-series) is distributed farther east over the Tenimber Islands and North Australia to the New Hebrides, but has also some allies in the Indo-Malayan Region; the *peranthus*-series occurs from Java to New Guinea, but is absent from Australia; another, *haliphron*-series, is found in Celebes and not in the Indo-Malayan Region: a fourth, *antiphates*-series, is found all over the Indo-Malayan Region, Celebes, and the Northern Moluccas, but is absent from the Southern Moluccas, Australia, New Guinea, and the islands farther east. Seven series reappear in the Indo-Malayan and Papuan Regions; while again seven series are found in the Indo-Malayan Region, three of them also in Celebes, all seven being absent from the Papuan Region.

---

* Compare also Doherty, *The Butterflies of Sumba and Sambawa*, in *Journ. As. Soc. Beng.* 1891; Pagenstecher, *Ueber die Lepidopteren von Sumba und Sambawa*, in *Jahrb. Nass. Ver. Nat.* 1896.

The lesser Sunda Islands have therefore not a single series of representatives which is purely Australian. From this fact we have to conclude that the immigration of the *Papilio* fauna cannot have taken place from Australia; and as the physiographical and meteorological conditions of the islands resemble in many respects more those of Northern Australia than those of the larger Sunda Islands, the reason why no Australian types immigrated cannot lie in the biological conditions of the islands, and hence must be accounted for by the assumption of another barrier against immigration. This barrier most probably was, at the time when the lesser Sunda Islands became first populated by Papilios, the same which we perceive at the present epoch, namely the wide Timor Sea separating Timor from Australia.

If we leave out of consideration as being indifferent the types which occur in the Indo-Malayan and Papuan Regions, there remain eight series of representatives which the lesser Sunda Islands have in common with the Indo-Malayan Region, and which are absent from Australia and New Guinea, four of them being represented also on Celebes, and one also on the Northern Moluccas; opposite these eight types stands one single Celebensian type that is absent from the Indo-Malayan Region. The Indo-Malayan element, therefore, is so strongly predominating that we must assume that there never existed any mechanical barrier of consequence preventing migration of the Papilios from the greater to the lesser Sunda Islands (or in the opposite direction).

Nevertheless there is a marked discrepancy in the fauna of the nearest of the larger Sunda Islands, Java, and the lesser Sunda Islands, as fourteen Javan types are not represented on any of the islands east of the Strait of Lombok, while six types occurring on the lesser Sunda Islands (except Lombok) are not known to have a representative on Java. From the fact that out of the eighteen series of representatives of the lesser Sunda Islands twelve occur on Java it is evident that the absence of fourteen Javan types from the lesser Sunda Islands, and the absence of six lesser Sunda Islands types (five of which are represented in other parts of the Indo-Malayan subregion) from Java, cannot acceptably be explained by the suggestion that there existed at a former period a very much wider strait between the lesser Sunda Islands and Java than there is now. And taking into account the *Papilio* fauna of Lombok alone,* which island has not a single *Papilio* type that is absent from Java, it is obvious that there is no evidence in favour of the assumption that the Strait of Lombok has changed in width since the appearance of the Papilios on the Malayan islands. If we exclude Lombok from the lesser Sunda Islands, and compare the *Papilio* fauna of the rest of the islands with that of Java, there is an important numerical discrepancy which amounts to more than 60 per cent. of the total number of the series of representative forms (as opposed to the total number of representative forms) inhabiting Java and the lesser Sunda Islands. As this amount † is very high compared with the numerical discrepancy and Papuan Regions; while again seven series are found in the Indo-Malayan Region, three of them also in Celebes, all seven being absent from the Papuan Region.

---

* The island has recently been visited by three explorers (W. Doherty, A. Everett, and H. Fruhstorfer).

† As Flores is lepidopterologically almost a blank the numbers may become quite different in consequence of the exploration of this large island. The absence of many types from small islands which are found on neighbouring large islands is quite natural, considering that the small islands do not afford so great a variety in the conditions of life as would be required by a multitude of diverse inhabitants.

The lesser Sunda Islands have therefore not a single series of representatives which is purely Australian. From this fact we have to conclude that the immigration of the *Papilio* fauna cannot have taken place from Australia; and as the physiographical and meteorological conditions of the islands resemble in many respects more those of Northern Australia than those of the larger Sunda Islands, the reason why no Australian types immigrated cannot lie in the biological conditions of the islands, and hence must be accounted for by the assumption of another barrier against immigration. This barrier most probably was, at the time when the lesser Sunda Islands became first populated by Papilios, the same which we perceive at the present epoch, namely the wide Timor Sea separating Timor from Australia.

If we leave out of consideration as being indifferent the types which occur in the Indo-Malayan and Papuan Regions, there remain eight series of representatives which the lesser Sunda Islands have in common with the Indo-Malayan Region, and which are absent from Australia and New Guinea, four of them being represented also on Celebes, and one also on the Northern Moluccas; opposite these eight types stands one single Celebensian type that is absent from the Indo-Malayan Region. The Indo-Malayan element, therefore, is so strongly predominating that we must assume that there never existed any mechanical barrier of consequence preventing migration of the Papilios from the greater to the lesser Sunda Islands (or in the opposite direction).

Nevertheless there is a marked discrepancy in the fauna of the nearest of the larger Sunda Islands, Java, and the lesser Sunda Islands, as fourteen Javan types are not represented on any of the islands east of the Strait of Lombok, while six types occurring on the lesser Sunda Islands (except Lombok) are not known to have a representative on Java. From the fact that out of the eighteen series of representatives of the lesser Sunda Islands twelve occur on Java it is evident that the absence of fourteen Javan types from the lesser Sunda Islands, and the absence of six lesser Sunda Islands types (five of which are represented in other parts of the Indo-Malayan subregion) from Java, cannot acceptably be explained by the suggestion that there existed at a former period a very much wider strait between the lesser Sunda Islands and Java than there is now. And taking into account the *Papilio* fauna of Lombok alone,* which island has not a single *Papilio* type that is absent from Java, it is obvious that there is no evidence in favour of the assumption that the Strait of Lombok has changed in width since the appearance of the Papilios on the Malayan islands. If we exclude Lombok from the lesser Sunda Islands, and compare the *Papilio* fauna of the rest of the islands with that of Java, there is an important numerical discrepancy which amounts to more than 60 per cent. of the total number of the series of representative forms (as opposed to the total number of representative forms) inhabiting Java and the lesser Sunda Islands. As this amount † is very high compared with the numerical discrepancy between Sumatra and Java (about 38 per cent. of the total number), and that between Sambawa and Timor (33 per cent. of the total number), and is not much inferior to the amount of discrepancy between the lesser Sunda Islands and Australia (65 per cent.), the lesser Sunda Islands can be considered as a faunistic district in opposition to the greater Sunda Islands and Australia; and it is very interesting to note that almost the same amount of numerical discrepancy must in the case of the lesser Sunda Islands and Java be accounted for by biological factors, while in the case of the lesser Sunda Islands and Australia the only acceptable explanation is the assumption of the existence of a geological barrier between Australia and Timor at the time when the lesser Sunda Islands became populated by Papilios.

---

* The island has recently been visited by three explorers (W. Doherty, A. Everett, and H. Fruhstorfer).

† As Flores is lepidopterologically almost a blank the numbers may become quite different in consequence of the exploration of this large island. The absence of many types from small islands which are found on neighbouring large islands is quite natural, considering that the small islands do not afford so great a variety in the conditions of life as would be required by a multitude of diverse inhabitants.

Turning now our attention to the second question proposed above to be discussed, we note that the characters of the forty-seven specifically or subspecifically different representative forms of *Papilio* occurring on the lesser Sunda Islands are such that forty-one of the forms are not found (as such) outside the group of islands, and hence are "peculiar" to the group. As these forty-one forms are so distributed that every island has some of its own and others in common with other islands of the group, while not a single form is identical on all the islands and at the same time distinguished by some peculiarity from the representative occurring on Java, Borneo, or in Australia, each island is in fact a small faunistic district, and the question arises whether the faunistic peculiarity exhibited by each island is not due, instead of to differences in the biological conditions existing on each island, to the mechanical separation of the islands by arms of sea, and hence finally would have to be referred to the action of geological factors. In the introduction we have endeavoured to show on *a priori* grounds that mechanical geographical separation as such cannot give rise to a new form: let us now consider the *a posteriori* reasons which speak against the origin of forms by mechanical isolation.

The widely distributed *Papilio sarpedon* has on the lesser Sunda Islands developed into three subspecies, one inhabiting Adonara, Sambawa, and Lombok—specimens from the latter island come very close to those from Java—a second found on Sumba, and a third occurring on Timor and Wetter. The external characters of the Timor form are such that it agrees in the shape of the hindwing best with the representative from Ceylon, in the breadth of the band of the forewing with the Australian form, and in the special shape of the anterior portion of the band with *monticolus* from Celebes, while it bears also great affinities to the forms from Sumba and Adonara. Setting apart all the reasons brought forward against the theory of isolation in the introduction, and conceding, for the sake of argument, that geographical isolation of aberrational specimens could lead to the origin of a new form of animal without the help of any biological factor, the combination of different affinities in the wing-characters of the Timorese, Sumbanese, or Adonaranese *sarpedon* forms might be thought due to the first specimens immigrated into each island having accidentally possessed the respective combination of characters. As a combination of characters such as exhibited by *P. sarpedon timorensis* is not found even in a less obvious degree in any specimen of *sarpedon* from the larger Sunda Islands and Australia we have seen, and therefore must be very rare, it is certainly scarcely probable that just such specimens which had that combination of characters should have happened to be the first to come to Timor: and this applies to all those localised forms, not only of the lesser Sunda Islands, but also of all other districts, the characters of which point in different directions. The improbability, however, between Sumatra and Java (about 38 per cent. of the total number), and that between Sambawa and Timor (33 per cent. of the total number), and is not much inferior to the amount of discrepancy between the lesser Sunda Islands and Australia (65 per cent.), the lesser Sunda Islands can be considered as a faunistic district in opposition to the greater Sunda Islands and Australia; and it is very interesting to note that almost the same amount of numerical discrepancy must in the case of the lesser Sunda Islands and Java be accounted for by biological factors, while in the case of the lesser Sunda Islands and Australia the only acceptable explanation is the assumption of the existence of a geological barrier between Australia and Timor at the time when the lesser Sunda Islands became populated by Papilios.

Turning now our attention to the second question proposed above to be discussed, we note that the characters of the forty-seven specifically or subspecifically different representative forms of *Papilio* occurring on the lesser Sunda Islands are such that forty-one of the forms are not found (as such) outside the group of islands, and hence are "peculiar" to the group. As these forty-one forms are so distributed that every island has some of its own and others in common with other islands of the group, while not a single form is identical on all the islands and at the same time distinguished by some peculiarity from the representative occurring on Java, Borneo, or in Australia, each island is in fact a small faunistic district, and the question arises whether the faunistic peculiarity exhibited by each island is not due, instead of to differences in the biological conditions existing on each island, to the mechanical separation of the islands by arms of sea, and hence finally would have to be referred to the action of geological factors. In the introduction we have endeavoured to show on *a priori* grounds that mechanical geographical separation as such cannot give rise to a new form: let us now consider the *a posteriori* reasons which speak against the origin of forms by mechanical isolation.

The widely distributed *Papilio sarpedon* has on the lesser Sunda Islands developed into three subspecies, one inhabiting Adonara, Sambawa, and Lombok—specimens from the latter island come very close to those from Java—a second found on Sumba, and a third occurring on Timor and Wetter. The external characters of the Timor form are such that it agrees in the shape of the hindwing best with the representative from Ceylon, in the breadth of the band of the forewing with the Australian form, and in the special shape of the anterior portion of the band with *monticolus* from Celebes, while it bears also great affinities to the forms from Sumba and Adonara. Setting apart all the reasons brought forward against the theory of isolation in the introduction, and conceding, for the sake of argument, that geographical isolation of aberrational specimens could lead to the origin of a new form of animal without the help of any biological factor, the combination of different affinities in the wing-characters of the Timorese, Sumbanese, or Adonaranese *sarpedon* forms might be thought due to the first specimens immigrated into each island having accidentally possessed the respective combination of characters. As a combination of characters such as exhibited by *P. sarpedon timorensis* is not found even in a less obvious degree in any specimen of *sarpedon* from the larger Sunda Islands and Australia we have seen, and therefore must be very rare, it is certainly scarcely probable that just such specimens which had that combination of characters should have happened to be the first to come to Timor; and this applies to all those localised forms, not only of the lesser Sunda Islands, but also of all other districts, the characters of which point in different directions. The improbability, however, changes into impossibility, if we take further into account the characters of the organs of copulation. We know from the researches laid down in the body of this paper that the genital armature varies quite independently from the wings and their markings, and that therefore the association of distinguishing characters relating to the wings with such found in the organs of copulation in morphological representatives has nothing to do with correlative development; in not a single case have we observed that a certain aberrational wing-character constantly reappearing among the individuals of a certain geographical form of *Papilio* is accompanied by an aberrational character in the organs of copulation. As, however, most geographical races are distinguished by characters of the wings and characters of the genital armature, it is evident that the explanation of the peculiarities in the wing-markings of a representative form by mechanical isolation of parent specimens which accidentally possessed those peculiarities (in a lower degree) is not an explanation of the presence of the peculiarities in the organs of copulation of the respective form. In order to account for the fact that *P. sarpedon timorensis* is (in the sexual armature of the *male*) different from all other forms of *sarpedon*, and comes in these organs nearest to the Ceylonese, Sumbanese, and Australian forms, and disagrees considerably with the representatives from Adonara, Sambawa, Lombok, and the Indo-Malayan Region, the theory of isolation would have to assume that the ancestral specimens of *timorensis*, no matter whether they immigrated into Timor from Australia or from the Malayan islands, must have been distinguished by a rare mixture of external peculiarities combined with an equally rare character in the organs of copulation. The rarity of such a combination in aberrations—in fact we never have found an aberrational individual in which the characters of both the wings and genital armature pointed in the direction of one representative form, instead of in different directions—is directly opposed to the fact that most geographical races exhibit that combination; this contradiction can only be solved by abandoning the assumption that the association of distinguishing characters of the wings with such of the sexual organs in localised forms is due to the geographical isolation of ancestral individuals which accidentally possessed such a combination of characters, and by accepting as the final cause of the presence of those characters the modifying action of isolated biological factors peculiar to the district where the peculiar form has originated.

If we thus attribute the existence of differences in the characters of the specimens of the same species inhabiting different districts to the presence of a difference in the biological factors of the districts, the degree of divergency of the forms is dependent on the degree of sensitiveness of the species to the action of the external biological factors, as maintained by Darwin, and after him by Weismann and others, in several places; further, on the intensity of the factors and the time they have been active; and thirdly, on the degree and duration of mechanical isolation as a prevention of the annihilating effect of intercrossing. As a difference in the physiological constitution of various species can be proved only by rearing them under exactly the same external conditions, and as we do not know in the case of species found in the same small island whether they actually do exist under the same external influences, it is not possible for us to decide with any degree of certainty whether the difference in the amount of divergency exhibited by the forms occurring in the same district is due to the different physiological constitution of the species differently affected, or to differences in the special external conditions under which each species perhaps exists. Nor are we able to say whether the greater diversity changes into impossibility, if we take further into account the characters of the organs of copulation. We know from the researches laid down in the body of this paper that the genital armature varies quite independently from the wings and their markings, and that therefore the association of distinguishing characters relating to the wings with such found in the organs of copulation in morphological representatives has nothing to do with correlative development; in not a single case have we observed that a certain aberrational wing-character constantly reappearing among the individuals of a certain geographical form of *Papilio* is accompanied by an aberrational character in the organs of copulation. As, however, most geographical races are distinguished by characters of the wings and characters of the genital armature, it is evident that the explanation of the peculiarities in the wing-markings of a representative form by mechanical isolation of parent specimens which accidentally possessed those peculiarities (in a lower degree) is not an explanation of the presence of the peculiarities in the organs of copulation of the respective form. In order to account for the fact that *P. sarpedon timorensis* is (in the sexual armature of the *male*) different from all other forms of *sarpedon*, and comes in these organs nearest to the Ceylonese, Sumbanese, and Australian forms, and disagrees considerably with the representatives from Adonara, Sambawa, Lombok, and the Indo-Malayan Region, the theory of isolation would have to assume that the ancestral specimens of *timorensis*, no matter whether they immigrated into Timor from Australia or from the Malayan islands, must have been distinguished by a rare mixture of external peculiarities combined with an equally rare character in the organs of copulation. The rarity of such a combination in aberrations—in fact we never have found an aberrational individual in which the characters of both the wings and genital armature pointed in the direction of one representative form, instead of in different directions—is directly opposed to the fact that most geographical races exhibit that combination; this contradiction can only be solved by abandoning the assumption that the association of distinguishing characters of the wings with such of the sexual organs in localised forms is due to the geographical isolation of ancestral individuals which accidentally possessed such a combination of characters, and by accepting as the final cause of the presence of those characters the modifying action of isolated biological factors peculiar to the district where the peculiar form has originated.

If we thus attribute the existence of differences in the characters of the specimens of the same species inhabiting different districts to the presence of a difference in the biological factors of the districts, the degree of divergency of the forms is dependent on the degree of sensitiveness of the species to the action of the external biological factors, as maintained by Darwin, and after him by Weismann and others, in several places; further, on the intensity of the factors and the time they have been active; and thirdly, on the degree and duration of mechanical isolation as a prevention of the annihilating effect of intercrossing. As a difference in the physiological constitution of various species can be proved only by rearing them under exactly the same external conditions, and as we do not know in the case of species found in the same small island whether they actually do exist under the same external influences, it is not possible for us to decide with any degree of certainty whether the difference in the amount of divergency exhibited by the forms occurring in the same district is due to the different physiological constitution of the species differently affected, or to differences in the special external conditions under which each species perhaps exists. Nor are we able to say whether the greater diversity exhibited by a certain form is due to the form having come under the influence of the biological factors of the respective district at an earlier period than another form which shows a less high degree of divergency, unless the sensitiveness of the forms has been tested by experiment. And again, the higher or lesser degree of geographical isolation, though often corresponding to the greater or lesser diversity of the isolated forms, is a factor the actual influence of which it is in a given case scarcely possible to estimate rightly. The great diversity of the representative of *Papilio peranthus* on the island of Sumba compared with the lesser diversity between the representatives inhabiting Java, Sambawa, Timor, Kalao and Djampea, Celebes, etc.; the high degree of specialisation of the representative of *Papilio memnon* on Timor compared with the lesser degree of divergency of the forms occurring on Sumba, Sambawa, Lombok, Java, etc.; the absence of a difference between some Lombok and Java forms of *Papilio* which on the other lesser Sunda Islands have developed divergently, compared with the presence of a difference in other Lombok forms; the great similarity between the specimens of *Papilio sarpedon* found in the area extending from N.W. India to Lombok, the gradual transition to the more divergent Adonara form, and the obvious divergency in the pattern and shape of the wings and the sexual armature (of the ♂) of the forms inhabiting Sumba, Timor, and Wetter respectively, compared with the great diversity of so many forms in N. India, Sumatra, Java, Lombok, Sambawa, and Adonara; the identity of the Malayan form of *Papilio aristeus* on the Philippines, Borneo, the lesser Sunda Islands, and the island of Djampea, compared with the great diversity exhibited in the same area by *Papilio memnon* and other species, and so on, are phenomena which seem to us most readily explainable by the surmise that the diverse species are sensitive in a different degree to the external biological factors; while the surprisingly great divergency of so many Celebensian Papilios must be attributed to a high intensity of the biological factors on that island and to a high degree of geographical isolation. However, it does not appear to us very probable that the narrow sea between Celebes and Borneo is a sufficiently effective barrier to prevent passive migration * of the widespread and common low-land Papilios of Borneo, such as *P. agamemnon*, *sarpedon*, *polytes*, etc., from Borneo to Celebes; and the same could be said of New Guinea, New Britain, and other islands. In fact the absence of intergraduate specimens between two representative forms in localities which are geographically close together—the intergradations may occur in other localities—makes it manifest to us that, as the effect of the biological factors would in these cases be annihilated, or at least much lessened, by specimens of the old stock coming into the country in consequence of the insufficiency of the geographical barrier, there must be another factor active to assist the external biological factors to such a degree that the migration of fresh individuals, if it does not take place very often, is not able to prevent divergent development. Now, recalling to mind the kind of variation in the scent-organs found to exist in a certain moth, as mentioned on p. 435, it is evident that where such a variation takes place in the geographical forms of a species the difference in the organs of smell and scent must be of great influence as preventing (to a certain extent) intercrossing between racial exhibited by a certain form is due to the form having come under the influence of the biological factors of the respective district at an earlier period than another form which shows a less high degree of divergency, unless the sensitiveness of the forms has been tested by experiment. And again, the higher or lesser degree of geographical isolation, though often corresponding to the greater or lesser diversity of the isolated forms, is a factor the actual influence of which it is in a given case scarcely possible to estimate rightly. The great diversity of the representative of *Papilio peranthus* on the island of Sumba compared with the lesser diversity between the representatives inhabiting Java, Sambawa, Timor, Kalao and Djampea, Celebes, etc.; the high degree of specialisation of the representative of *Papilio memnon* on Timor compared with the lesser degree of divergency of the forms occurring on Sumba, Sambawa, Lombok, Java, etc.; the absence of a difference between some Lombok and Java forms of *Papilio* which on the other lesser Sunda Islands have developed divergently, compared with the presence of a difference in other Lombok forms; the great similarity between the specimens of *Papilio sarpedon* found in the area extending from N.W. India to Lombok, the gradual transition to the more divergent Adonara form, and the obvious divergency in the pattern and shape of the wings and the sexual armature (of the ♂) of the forms inhabiting Sumba, Timor, and Wetter respectively, compared with the great diversity of so many forms in N. India, Sumatra, Java, Lombok, Sambawa, and Adonara; the identity of the Malayan form of *Papilio aristeus* on the Philippines, Borneo, the lesser Sunda Islands, and the island of Djampea, compared with the great diversity exhibited in the same area by *Papilio memnon* and other species, and so on, are phenomena which seem to us most readily explainable by the surmise that the diverse species are sensitive in a different degree to the external biological factors; while the surprisingly great divergency of so many Celebensian Papilios must be attributed to a high intensity of the biological factors on that island and to a high degree of geographical isolation. However, it does not appear to us very probable that the narrow sea between Celebes and Borneo is a sufficiently effective barrier to prevent passive migration * of the widespread and common low-land Papilios of Borneo, such as *P. agamemnon, sarpedon, polytes*, etc., from Borneo to Celebes; and the same could be said of New Guinea, New Britain, and other islands. In fact the absence of intergraduate specimens between two representative forms in localities which are geographically close together—the intergradations may occur in other localities—makes it manifest to us that, as the effect of the biological factors would in these cases be annihilated, or at least much lessened, by specimens of the old stock coming into the country in consequence of the insufficiency of the geographical barrier, there must be another factor active to assist the external biological factors to such a degree that the migration of fresh individuals, if it does not take place very often, is not able to prevent divergent development. Now, recalling to mind the kind of variation in the scent-organs found to exist in a certain moth, as mentioned on p. 435, it is evident that where such a variation takes place in the geographical forms of a species the difference in the organs of smell and scent must be of great influence as preventing (to a certain extent) intercrossing between racial forms, so that the distinguishing characters can accumulate in spite of the occasional immigration of specimens of the old stock. As we shall have to deal with this kind of physiological selection, which in fact is a kind of sexual selection, in another place when treating upon the variation of glandular organs in *Lepidoptera*, we do not now enter upon a discussion of that factor. The variation of *Lepidoptera* explained in the present paper points, however, to a further factor being active, the importance of which as a means of prevention of intercrossing has been recognised as far back as 1849, and we shall try now, on the ground of our researches, to estimate the influence of geographical polymorphism in the sexual organs upon the divergent development of the *Lepidoptera*.

---

* Passive migration by means of hurricanes seems to occur often among birds, as the records of foreign birds found in England prove; in the case of *Lepidoptera* the power of resistance is certainly slighter, but the effect of migration in respect to intercrossing with specimens of the same species in the new locality will often be annihilated in consequence of the new-comers having too much suffered to be fit for propagation.

---

* Passive migration by means of hurricanes seems to occur often among birds, as the records of foreign birds found in England prove; in the case of *Lepidoptera* the power of resistance is certainly slighter, but the effect of migration in respect to intercrossing with specimens of the same species in the new locality will often be annihilated in consequence of the new-comers having too much suffered to be fit for propagation.

C. MECHANICAL SELECTION.

The genital armature of *Lepidoptera* has the function of a special prehensile apparatus during copulation. As such apparatus is found in all *Lepidoptera*, we can conclude that its function is of high importance for the act of copulation. When, however, a physiologically important organ is found to be of a different structure in every two species, it is likewise correct to conclude that the difference in the structure has some physiological significance. Hence we think that the inference to be drawn from the fact that the copulatory organs are different in different species has to be that the specialisation in structure means a specialisation in the function as prehensile organ—*i.e.* that, as with the help of the apparatus the *male* has to take a hold on the *female* and the *female* on the *male*, the organs of the sexes of the same species are best adapted to each other. This inference implies that specimens of diverse species can less easily copulate than specimens of the same species, and that there might be cases in which copulation between different species would be impossible in consequence of the highly divergent specialisation of the organs of copulation. A similar view has been held by the earlier writers on the subject, Siebold[*] and Dufour,[†] the latter giving expression to his opinion in the well-known sentence that "*l'armure copulatrice . . . est la garantie de la conservation des types, la sauvegarde de la légitimité de l'espèce.*"

The different development of the organs of copulation is here alleged to be a means of prevention of intercrossing between specifically different specimens, and the same has more recently been said by Escherich,[‡] Hoffer,[§] and others. Though we know from experience that Escherich's assertion that an effective copulation between diverse species is never possible is erroneous, and that therefore Verhoeff[||] is right in rejecting this part of Escherich's theory, it remains nevertheless evident that under the premiss that the *male* and *female* of one species really are adapted to each other in respect to the genital armature, specimens which are not adapted to each other cannot so easily unite in copulation, and that even when a union is effected the penis will sometimes be prevented from entering the vagina in consequence of the vaginal armature, to which the organs of that *male* are not adapted, being a mechanical barrier. Before, however, this conclusion can be accepted, it has to be ascertained whether the actual structure of the *female* and *male* genital armature is in accordance with the above premiss.

Gosse[¶] was quite right in expecting to find that "every peculiarity in the forms, so that the distinguishing characters can accumulate in spite of the occasional immigration of specimens of the old stock. As we shall have to deal with this kind of physiological selection, which in fact is a kind of sexual selection, in another place when treating upon the variation of glandular organs in *Lepidoptera*, we do not now enter upon a discussion of that factor. The variation of *Lepidoptera* explained in the present paper points, however, to a further factor being active, the importance of which as a means of prevention of intercrossing has been recognised as far back as 1849, and we shall try now, on the ground of our researches, to estimate the influence of geographical polymorphism in the sexual organs upon the divergent development of the *Lepidoptera*.

---

[*] *Vergl. Anat.* Berlin, 1848. § 354. note 2.

[†] *Ann. Sc. Nat.* (3). I. 1844. p. 253.

[‡] *Verh. z. b. Ges. Wien.* 1892. p. 234.

[§] *Mitth. Nat. Ver. Steiermark.* 1888.

[||] *Ent. Nachr.* 1893. p. 44.

[¶] *Trans. Linn. Soc. Lond.* (2). II. 1883. p. 279.

C. Mechanical Selection.

The genital armature of *Lepidoptera* has the function of a special prehensile apparatus during copulation. As such apparatus is found in all *Lepidoptera*, we can conclude that its function is of high importance for the act of copulation. When, however, a physiologically important organ is found to be of a different structure in every two species, it is likewise correct to conclude that the difference in the structure has some physiological significance. Hence we think that the inference to be drawn from the fact that the copulatory organs are different in different species has to be that the specialisation in structure means a specialisation in the function as prehensile organ—*i.e.* that, as with the help of the apparatus the *male* has to take a hold on the *female* and the *female* on the *male*, the organs of the sexes of the same species are best adapted to each other. This inference implies that specimens of diverse species can less easily copulate than specimens of the same species, and that there might be cases in which copulation between different species would be impossible in consequence of the highly divergent specialisation of the organs of copulation. A similar view has been held by the earlier writers on the subject, Siebold[*] and Dufour,[†] the latter giving expression to his opinion in the well-known sentence that "*l'armure copulatrice . . . est la garantie de la conservation des types, la sauvegarde de la légitimité de l'espèce.*"

The different development of the organs of copulation is here alleged to be a means of prevention of intercrossing between specifically different specimens, and the same has more recently been said by Escherich,[‡] Hoffer,[§] and others. Though we know from experience that Escherich's assertion that an effective copulation between diverse species is never possible is erroneous, and that therefore Verhoeff[‖] is right in rejecting this part of Escherich's theory, it remains nevertheless evident that under the premiss that the *male* and *female* of one species really are adapted to each other in respect to the genital armature, specimens which are not adapted to each other cannot so easily unite in copulation, and that even when a union is effected the penis will sometimes be prevented from entering the vagina in consequence of the vaginal armature, to which the organs of that *male* are not adapted, being a mechanical barrier. Before, however, this conclusion can be accepted, it has to be ascertained whether the actual structure of the *female* and *male* genital armature is in accordance with the above premiss.

Gosse[¶] was quite right in expecting to find that "every peculiarity in the

---

[*] *Vergl. Anat.* Berlin, 1848. § 354. note 2.

[†] *Ann. Sc. Nat.* (3). I. 1844. p. 253.

[‡] *Verh. z. b. Ges. Wien.* 1892. p. 234.

[§] *Mitth. Nat. Ver. Steiermark.* 1888.

[‖] *Ent. Nachr.* 1893. p. 44.

[¶] *Trans. Linn. Soc. Lond.* (2). II. 1883. p. 279.

prehensile organs of the *male* would have a corresponding peculiarity in that part of the *female* body which they were formed to grasp," but he failed to discover "the corresponding peculiarity in the *female*," as he laboured under the erroneous assumption that "it is the *exterior* of the final segments of the *female* abdomen that are seized *in coitu*." We have been able to show in the body of this paper that the *male* claspers seize in copulation the protruding vaginal bulb, taking hold on chitinised folds and ridges, and not the terminal segments ; and we have further been able to demonstrate the following two important points :—

(1) We have a pair of *Papilio memnon* united *in coitu*, from which we see clearly that the harpe of the *male* fits exactly the lateral ridge of the vaginal bulb of the *female*, while the high and broad processes at the mouth of the vagina, besides being a guide to the penis, take hold on the internal parts of the ninth segment of the *male*. When uniting artificially *males* and *females* of other species, we find that the organs of one sex fit those of the other of the same species, while the copulatory organs of different species, for instance of a *male* of *P. machaon* and a *female* of *P. podalirius*, or of *memnon* and *helenus*, do not fit each other. We are therefore justified in concluding that the organs of the sexes of the same species are better adapted to each other than to the organs of other species.

(2) The vaginal armature is in every species of *Papilio* examined different from that of every other species examined. As our researches, only part of which have been laid down in this paper, relate to a great many species of various groups of *Papilio* and other *Lepidoptera*, we can safely say that the *females* of every species are, like the *males*, in the sexual armature distinguished from the *females* of every other species. A comparison of the figures on Pl. XIX. will show that the divergency between the apparatus of representatives of diverse groups is in every respect so great, that it is readily conceivable that a *male* the apparatus of which is adapted to such organs as represented by f. 181 cannot effectively copulate with a *female* the organs of which are so different as those represented by f. 163, 179, or 182.

The position of the vaginal orifice and the lateral fold of the vaginal bulb, the number, length, and position of the ridges and processes at the orifice of the vagina, and the development of the eighth segment of the *female*, as well as the special structure of the clasping organs of the *male*, are in diverse groups of *Papilio* so widely different that there can be no doubt that the divergency in the organs of copulation has rightly been interpreted by Siebold as a means of prevention of intercrossing. It is obvious that the more the organs of different species resemble each other the less they will be able to prevent copulation. In closely allied species, therefore, the effect of this mechanical barrier against intercrossing will generally be less great than in the case of more diverse forms; but we must recall to mind that even in the most closely related species, such as *Papilio euchenor* and *depilis* (f. 51 and 65), the organs of copulation, though built up after the same plan, can in the position and direction of the spines, hooks, and ridges of the harpe be so different that the prehensile organs of the *male* come in contact during copulation with quite different points of the vaginal region of the *female*, and that it is accordingly also in such cases obvious that an intercrossing is not possible without violence. In groups of *Lepidoptera* in which the genital armature is very simple the effect as a mechanical barrier must necessarily be very slight ; this seems to us to be one reason why specimens of diverse species of *Saturnidae*, for instance, copulate much easier than is the case with specifically different individuals in other groups.

prehensile organs of the *male* would have a corresponding peculiarity in that part of the *female* body which they were formed to grasp," but he failed to discover "the corresponding peculiarity in the *female*," as he laboured under the erroneous assumption that "it is the *exterior* of the final segments of the *female* abdomen that are seized *in coitu*." We have been able to show in the body of this paper that the *male* claspers seize in copulation the protruding vaginal bulb, taking hold on chitinised folds and ridges, and not the terminal segments ; and we have further been able to demonstrate the following two important points :—

(1) We have a pair of *Papilio memnon* united *in coitu*, from which we see clearly that the harpe of the *male* fits exactly the lateral ridge of the vaginal bulb of the *female*, while the high and broad processes at the mouth of the vagina, besides being a guide to the penis, take hold on the internal parts of the ninth segment of the *male*. When uniting artificially *males* and *females* of other species, we find that the organs of one sex fit those of the other of the same species, while the copulatory organs of different species, for instance of a *male* of *P. machaon* and a *female* of *P. podalirius*, or of *memnon* and *helenus*, do not fit each other. We are therefore justified in concluding that the organs of the sexes of the same species are better adapted to each other than to the organs of other species.

(2) The vaginal armature is in every species of *Papilio* examined different from that of every other species examined. As our researches, only part of which have been laid down in this paper, relate to a great many species of various groups of *Papilio* and other *Lepidoptera*, we can safely say that the *females* of every species are, like the *males*, in the sexual armature distinguished from the *females* of every other species. A comparison of the figures on Pl. XIX. will show that the divergency between the apparatus of representatives of diverse groups is in every respect so great, that it is readily conceivable that a *male* the apparatus of which is adapted to such organs as represented by f. 181 cannot effectively copulate with a *female* the organs of which are so different as those represented by f. 163, 179, or 182.

The position of the vaginal orifice and the lateral fold of the vaginal bulb, the number, length, and position of the ridges and processes at the orifice of the vagina, and the development of the eighth segment of the *female*, as well as the special structure of the clasping organs of the *male*, are in diverse groups of *Papilio* so widely different that there can be no doubt that the divergency in the organs of copulation has rightly been interpreted by Siebold as a means of prevention of intercrossing. It is obvious that the more the organs of different species resemble each other the less they will be able to prevent copulation. In closely allied species, therefore, the effect of this mechanical barrier against intercrossing will generally be less great than in the case of more diverse forms; but we must recall to mind that even in the most closely related species, such as *Papilio euchenor* and *depilis* (f. 51 and 65), the organs of copulation, though built up after the same plan, can in the position and direction of the spines, hooks, and ridges of the harpe be so different that the prehensile organs of the *male* come in contact during copulation with quite different points of the vaginal region of the *female*, and that it is accordingly also in such cases obvious that an intercrossing is not possible without violence. In groups of *Lepidoptera* in which the genital armature is very simple the effect as a mechanical barrier must necessarily be very slight ; this seems to us to be one reason why specimens of diverse species of *Saturnidae*, for instance, copulate much easier than is the case with specifically different individuals in other groups.

Notwithstanding it is manifest that the difficulty to obtain hybrids is in many cases to be attributed to the diverse development of the copulatory organs, the question is of very little importance as long as we take into account only an intercrossing between species and species. According to our definition, specifically distinct animals or plants cannot fuse together; the appearance of hybrids has no influence on the evolution of the species which have produced them, though they may obscure the fact of the specific distinctness of the parents.* The barrier between species is the degree of diversity already attained, and as this barrier is absolute, the presence of any other barrier must be indifferent. The question as to the evolutionistic influence of the peculiar development of the copulatory organs, therefore, does not relate to those forms which have already attained that degree of diversity which renders a fusion with other forms impossible, but to those lower degrees of diversity which are still able to fuse together under favourable circumstances. Hence we have to inquire whether the variation of the copulatory organs within the limits of a species is such that the difference in the organs in question between varieties of the same species can be thought to be a barrier against the sexual intercourse between the varieties.

The effect of the divergency of the copulatory organs in respect to prevention of intercrossing can very well be compared with that of geographical isolation, as the effect of both the morphological and the geographical factor depends on the extent of the mechanical barrier. The Atlantic Ocean is certainly an effective barrier between the Nearctic and Palaearctic Regions, although even such a wide sea cannot absolutely prevent a migration from one region to the other; the Ganges Valley which separates the North Indian from the South Indian fauna, and the straits between the various islands of the Indo-Australian Archipelago, are barriers which render the occurrence of an intercrossing between specimens born on the opposite sides of the barrier, though by no means impossible, doubtless very rare; in fact every barrier which isolates to any degree, however small the degree may be, a number of specimens *A* from other specimens *B* renders the intercourse of the two sets of individuals with one another less probable than the copulation of the specimens of each set *inter se*, and hence is a barrier against intercrossing. If, therefore, the varieties of the same species exhibit in both sexes any diversity in the the organs of copulation, we can rightly infer that this diversity will act like a geographical barrier, isolating the varieties from one another to a certain extent according as the anatomical diversity is great or slight. As our researches have proved that the premiss of this conclusion is correct as regards the Eastern Papilios, namely that there are varieties which differ in the genital armature from other varieties of the same species in both sexes, it is manifest that the diversity in the genital armature of the Papilios has a great bearing upon the divergent development of the varieties.

We have found that there is individual and geographical variation in the genital armature of the Eastern Papilios. As regards individual variation, it is obvious that specimens which have any marked peculiarity in the prehensile organs, additional hooks or ridges, in which they deviate from the normal, will be at a disadvantage in

---

* As besides the mechanical barrier against intercrossing there is, in most species with highly developed organs of sense, a psychological barrier active, hybrids must in the state of nature be very rare in comparison with the number of specimens which are not hybrids. Specimens connecting two supposed distinct species have not rarely been treated as hybrids, though the natural conclusion from the regular occurrence of such intergradations would be that the supposed distinct species form one, di- or polymorphic, species, provided that the reverse has not been *proved*.

Notwithstanding it is manifest that the difficulty to obtain hybrids is in many cases to be attributed to the diverse development of the copulatory organs, the question is of very little importance as long as we take into account only an intercrossing between species and species. According to our definition, specifically distinct animals or plants cannot fuse together; the appearance of hybrids has no influence on the evolution of the species which have produced them, though they may obscure the fact of the specific distinctness of the parents.* The barrier between species is the degree of diversity already attained, and as this barrier is absolute, the presence of any other barrier must be indifferent. The question as to the evolutionistic influence of the peculiar development of the copulatory organs, therefore, does not relate to those forms which have already attained that degree of diversity which renders a fusion with other forms impossible, but to those lower degrees of diversity which are still able to fuse together under favourable circumstances. Hence we have to inquire whether the variation of the copulatory organs within the limits of a species is such that the difference in the organs in question between varieties of the same species can be thought to be a barrier against the sexual intercourse between the varieties.

The effect of the divergency of the copulatory organs in respect to prevention of intercrossing can very well be compared with that of geographical isolation, as the effect of both the morphological and the geographical factor depends on the extent of the mechanical barrier. The Atlantic Ocean is certainly an effective barrier between the Nearctic and Palaearctic Regions, although even such a wide sea cannot absolutely prevent a migration from one region to the other; the Ganges Valley which separates the North Indian from the South Indian fauna, and the straits between the various islands of the Indo-Australian Archipelago, are barriers which render the occurrence of an intercrossing between specimens born on the opposite sides of the barrier, though by no means impossible, doubtless very rare; in fact every barrier which isolates to any degree, however small the degree may be, a number of specimens *A* from other specimens *B* renders the intercourse of the two sets of individuals with one another less probable than the copulation of the specimens of each set *inter se*, and hence is a barrier against intercrossing. If, therefore, the varieties of the same species exhibit in both sexes any diversity in the the organs of copulation, we can rightly infer that this diversity will act like a geographical barrier, isolating the varieties from one another to a certain extent according as the anatomical diversity is great or slight. As our researches have proved that the premiss of this conclusion is correct as regards the Eastern Papilios, namely that there are varieties which differ in the genital armature from other varieties of the same species in both sexes, it is manifest that the diversity in the genital armature of the Papilios has a great bearing upon the divergent development of the varieties.

We have found that there is individual and geographical variation in the genital armature of the Eastern Papilios. As regards individual variation, it is obvious that specimens which have any marked peculiarity in the prehensile organs, additional hooks or ridges, in which they deviate from the normal, will be at a disadvantage in respect to propagation compared with the normal specimens in which copulation is more facilitated ; monstrosities and sports in respect to the genital armature, in short every specimen with an anomalous development of the organs of copulation is less favoured than the rest of the individuals. Such abnormal individuals have, therefore, the same position in the struggle for propagation, as in the struggle for existence those specimens have which are less adapted to the circumstances of life than their cospecific rivals. If it is right to conclude in the latter case that the struggle for existence leads in the long run to a survival of the fit (*Romanes*), we can apply the same inference to our special question and say that the specimens abnormal in the genital organs will in the struggle for propagation succumb, and that consequently the anomalies in the organs of copulation will become rarer and rarer, the individuals acquiring gradually by breeding in and in the same form of prehensile organs, comparatively few specimens deviating widely from the normal. It is apparent that the mechanical selection thus effected will end in a comparatively great constancy of the prehensile apparatus.* A number of the forms of *Papilio* dealt with in this paper have attained a remarkably high degree of constancy in the genital armature, for instance several forms of *P. sarpedon* and *P. aristeus*, *P. alcinous confusus*. As the conclusion applies to every segregate form of *Papilio*, it is evident that, when a species develops divergently into geographical races, each race (or some of them) can, and will, acquire a special normal form of the genital armature, if the evolutionistic factors of the locality affect the organs of copulation. Many species have not yet attained that degree of divergent ramification. The geographical forms of *Papilio aegeus*, *machaon*, some of the races of *P. sarpedon*, namely *sarpedon sarpedon* and *sarpedon semifasciatus*, the two eastern races of *P. aristeus*, *P. aristeus aristeus* and *P. aristeus parmatus*, and others, we have found to be identical or almost so with one another in the genital armature. In the geographical forms of other species the specialisation in the prehensile organs is already visible, but not very conspicuous, as in *P. cloanthus clymenus* and *P. cloanthus cloanthus* ; while in others again the degree of divergency in the organs of copulation of geographical races is so high that the normal of one form differs from the normal of the other so much that the one stands far outside the usual limits of variation of the other. Now, when it happens that forms so diverse in the genital armature inhabit neighbouring districts, as is the case with *P. sarpedon teredon* (S. India), *P. sarpedon sarpedon* (N. India to the Philippines and Java), and *P. sarpedon milon* (Celebes) ; *P. alcinous confusus* (China and Formosa) and *P. alcinous loochooanus* (Loo Choo Islands) ; *P. bathycles chiron* (N. India to Burma) and *P. bathycles bathycloides* (Malacca), it is manifest that the occasional (passive or active) migration of specimens from one district to the other, which we must concede to occur, as otherwise the wide range of many species would not be explainable, can have no great retarding effect on the divergent development of the forms, since an effective copulation of the immigrants with the occupants of the district is improbable, and as further, if copulation should occasionally be effective, the characters of the descendants of the new-comers will soon get swamped away by mechanical selection. Thus it is conceivable that, when a certain degree of divergency is attained by geographical races, mechanical selection will greatly help to accelerate evolution, and that it is able to prevent retrograde development when the geographical barrier which formerly separated two forms has, in consequence of respect to propagation compared with the normal specimens in which copulation is more facilitated ; monstrosities and sports in respect to the genital armature, in short every specimen with an anomalous development of the organs of copulation is less favoured than the rest of the individuals. Such abnormal individuals have, therefore, the same position in the struggle for propagation, as in the struggle for existence those specimens have which are less adapted to the circumstances of life than their cospecific rivals. If it is right to conclude in the latter case that the struggle for existence leads in the long run to a survival of the fit (*Romanes*), we can apply the same inference to our special question and say that the specimens abnormal in the genital organs will in the struggle for propagation succumb, and that consequently the anomalies in the organs of copulation will become rarer and rarer, the individuals acquiring gradually by breeding in and in the same form of prehensile organs, comparatively few specimens deviating widely from the normal. It is apparent that the mechanical selection thus effected will end in a comparatively great constancy of the prehensile apparatus.* A number of the forms of *Papilio* dealt with in this paper have attained a remarkably high degree of constancy in the genital armature, for instance several forms of *P. sarpedon* and *P. aristeus*, *P. alcinous confusus*. As the conclusion applies to every segregate form of *Papilio*, it is evident that, when a species develops divergently into geographical races, each race (or some of them) can, and will, acquire a special normal form of the genital armature, if the evolutionistic factors of the locality affect the organs of copulation. Many species have not yet attained that degree of divergent ramification. The geographical forms of *Papilio aegeus*, *machaon*, some of the races of *P. sarpedon*, namely *sarpedon sarpedon* and *sarpedon semifasciatus*, the two eastern races of *P. aristeus*, *P. aristeus aristeus* and *P. aristeus parmatus*, and others, we have found to be identical or almost so with one another in the genital armature. In the geographical forms of other species the specialisation in the prehensile organs is already visible, but not very conspicuous, as in *P. cloanthus clymenus* and *P. cloanthus cloanthus* ; while in others again the degree of divergency in the organs of copulation of geographical races is so high that the normal of one form differs from the normal of the other so much that the one stands far outside the usual limits of variation of the other. Now, when it happens that forms so diverse in the genital armature inhabit neighbouring districts, as is the case with *P. sarpedon teredon* (S. India), *P. sarpedon sarpedon* (N. India to the Philippines and Java), and *P. sarpedon milon* (Celebes); *P. alcinous confusus* (China and Formosa) and *P. alcinous loochooanus* (Loo Choo Islands) ; *P. bathycles chiron* (N. India to Burma) and *P. bathycles bathycloides* (Malacca), it is manifest that the occasional (passive or active) migration of specimens from one district to the other, which we must concede to occur, as otherwise the wide range of many species would not be explainable, can have no great retarding effect on the divergent development of the forms, since an effective copulation of the immigrants with the occupants of the district is improbable, and as further, if copulation should occasionally be effective, the characters of the descendants of the new-comers will soon get swamped away by mechanical selection. Thus it is conceivable that, when a certain degree of divergency is attained by geographical races, mechanical selection will greatly help to accelerate evolution, and that it is able to prevent retrograde development when the geographical barrier which formerly separated two forms has, in consequence of geological revolutions, become so changed that the isolation is much more incomplete than it formerly was. And when the comparatively great diversity in the organs of copulation has become so constant that intergradations in these organs between two respective subspecies seldom occur in the area occupied by these forms, though the subspecies may be connected with one another by intergraduate forms inhabiting other districts, it is possible that, when the districts of the two subspecies, if geographically close together, like the Bornean and Philippine Islands, become so extended that they overlap, the two diverse subspecies may live together without immediate and complete fusion.

---

* As besides the mechanical barrier against intercrossing there is, in most species with highly developed organs of sense, a psychological barrier active, hybrids must in the state of nature be very rare in comparison with the number of specimens which are not hybrids. Specimens connecting two supposed distinct species have not rarely been treated as hybrids, though the natural conclusion from the regular occurrence of such intergradations would be that the supposed distinct species form one, di- or polymorphic, species, provided that the reverse has not been *proved*.

---

* Marked dimorphism in the organs of copulation to which the variation of the organs could also lead does not seem to occur ; see p. 499.

---

* Marked dimorphism in the organs of copulation to which the variation of the organs could also lead does not seem to occur ; see p. 499.

It will have been noted that the effect attributed to mechanical selection is twofold. The variation of the genital armature caused by transmuting factors of any kind is so guided by mechanical selection that every incipient species will acquire a special armature of its own. As the variation of the organs of copulation is independent of that of the wing-pattern, mechanical selection does not directly affect the latter; but its indirect influence must be of importance, when the special genital armature acquired by mechanical selection has become so specialised that it is, like local isolation, a means of prevention of intercrossing.

In consequence of the demonstration of individual and geographical variation of the organs of copulation it becomes very probable that Eimer's [*] interesting suggestion is correct, that the variation of a species concerns also egg and sperm. If geographical and individual variation in these cells would be demonstrable as in the case of the ectodermal sexual organs, we should most probably find that the variation in the size and form of the sperm and in the structure of the micropyle apparatus [†] of the egg is independent of the characters of the wing and sexual armature, and that accordingly similar conclusions could be drawn as in the case of the organs of copulation. As diversity in sperm and egg would partly or totally prevent fecundation, infertility between certain individuals of the same race and between the specimens of diverse races would be the result of the variation, and hence the demonstration of the occurrence of such variation would give an actual base to Romanes's theory of physiological selection, and thus supply one explanation of that hitherto unsolved question how the general infertility between species has come about.

"The real difficulty," says Darwin,[‡] "in our present subject is not, as it appears to me, why domestic varieties have not become mutually infertile when crossed, but why this has so generally occurred with natural varieties, as soon as they have been permanently modified in a sufficient degree to take rank as a species. We are far from precisely knowing the cause; nor is this surprising, seeing how profoundly ignorant we are in regard to the normal and abnormal action of the reproductive system."

We observe that the cause of infertility adduced by us would not be physiological diversity, but mechanical impossibility of fertilisation. Mechanical selection acting in a similar way as in the case of the organs of copulation in the direction of adapting within each race sperm to egg by excluding extreme varietal specimens from propagation, would raise a barrier between the diverse subspecies which would admit an independent development ending in specific distinctness of mutually infertile forms. Mechanical selection acts upon variation caused by other factors, and is, therefore, like mechanical geographical isolation, a preservative, not a productive factor.

[*] *Artb. bei Schmett.* II. 1895. p. 15.

[†] Standfuss, *Handb. f. Schmetterlingssammler* 1896.

[‡] *Origin of Species* 6th ed. London, 1888. p. 36.

geological revolutions, become so changed that the isolation is much more incomplete than it formerly was. And when the comparatively great diversity in the organs of copulation has become so constant that intergradations in these organs between two respective subspecies seldom occur in the area occupied by these forms, though the subspecies may be connected with one another by intergraduate forms inhabiting other districts, it is possible that, when the districts of the two subspecies, if geographically close together, like the Bornean and Philippine Islands, become so extended that they overlap, the two diverse subspecies may live together without immediate and complete fusion.

It will have been noted that the effect attributed to mechanical selection is twofold. The variation of the genital armature caused by transmuting factors of any kind is so guided by mechanical selection that every incipient species will acquire a special armature of its own. As the variation of the organs of copulation is independent of that of the wing-pattern, mechanical selection does not directly affect the latter; but its indirect influence must be of importance, when the special genital armature acquired by mechanical selection has become so specialised that it is, like local isolation, a means of prevention of intercrossing.

In consequence of the demonstration of individual and geographical variation of the organs of copulation it becomes very probable that Eimer's [*] interesting suggestion is correct, that the variation of a species concerns also egg and sperm. If geographical and individual variation in these cells would be demonstrable as in the case of the ectodermal sexual organs, we should most probably find that the variation in the size and form of the sperm and in the structure of the micropyle apparatus [†] of the egg is independent of the characters of the wing and sexual armature, and that accordingly similar conclusions could be drawn as in the case of the organs of copulation. As diversity in sperm and egg would partly or totally prevent fecundation, infertility between certain individuals of the same race and between the specimens of diverse races would be the result of the variation, and hence the demonstration of the occurrence of such variation would give an actual base to Romanes's theory of physiological selection, and thus supply one explanation of that hitherto unsolved question how the general infertility between species has come about.

"The real difficulty," says Darwin,[‡] "in our present subject is not, as it appears to me, why domestic varieties have not become mutually infertile when crossed, but why this has so generally occurred with natural varieties, as soon as they have been permanently modified in a sufficient degree to take rank as a species. We are far from precisely knowing the cause; nor is this surprising, seeing how profoundly ignorant we are in regard to the normal and abnormal action of the reproductive system."

We observe that the cause of infertility adduced by us would not be physiological diversity, but mechanical impossibility of fertilisation. Mechanical selection acting in a similar way as in the case of the organs of copulation in the direction of adapting within each race sperm to egg by excluding extreme varietal specimens from propagation, would raise a barrier between the diverse subspecies which would admit an independent development ending in specific distinctness of mutually infertile forms. Mechanical selection acts upon variation caused by other factors, and is, therefore, like mechanical geographical isolation, a preservative, not a productive factor.

---

[*] *Artb. bei Schmett.* II. 1895. p. 15.

[†] Standfuss, *Handb. f. Schmetterlingssammler* 1896.

[‡] *Origin of Species* 6th ed. London, 1888. p. 36.

LIST OF INSECTS MENTIONED IN THIS PAPER.

Acherontia atropos, in Hübner, *Samml. Eur. Schm.* II. *Sphing.* f. 63 (1798-1805).
Callimorpha dominula dominula, in Esper. *Eur. Schm.* IV. t. 83. f. 1. 2 (1786).
,, *dominula persona*, in Hübner, *Samml. Eur. Schm.* III. f. 319-322 (1798—1805).
Euploea rhadamanthus, in Distant, *Rhop. Mal.* 1885. t. 4. f. 4. 5 (as *diocletianus*).
Gonopteryx cleopatra, in Hübner, *Samml. Eur. Schm.* f. 445. 446 (1798—1805).
,, *rhamni*, *ibid.* f. 442-444.
Hepialus humuli hethlandicus, in *Entomol.* 1880. t. 3.
,, *humuli humuli*, in Esper, *Eur. Schmett.* IV. t. 80. f. 1 (♂). 2 (♀). (1786).
Ornithoptera, see *Troides*.
Papilio aegeus, in Novit. Zool. 1895. p. 304.
,, *aegeus adrastus*, in *Reise Novara, Lep.* I. t. 16. f. a (1865).
,, *aegeus aegeus*, in Staud. & Schatz, *Exot. Schmett.* I. t. 4 (1884).
,, *aegeus bismarckianus*, in Novit. Zool. 1895. p. 308.
,, *aegeus keianus*, in Novit. Zool. 1896. p. 422.
,, *aegeus ormenus*, in Novit. Zool. 1895. p. 306.
,, *aegeus ormenus* ♂-ab. *ormenus*, in *Voyage Coquille, Ins.* t. 14. f. 3 (1829).
,, *aegeus ormenus* ♂-ab. *othello*, in Novit. Zool. 1894. p. 332. n. 3.
,, *aegeus ormenus* ♂-ab. *pandion*, in *Trans. Linn. Soc. Lond.* XXV. p. 56. n. 72 (1865).
,, *agamemnon*, in Novit. Zool. 1895. p. 417.
,, *agamemnon argynnus*, in *Ann. Mag. N. H.* (6). II. p. 235 (1888).
,, *agamemnon neopommeranius*, in *Berl. Ent. Zeitschr.* XXXI. t. 6. f. 4 (1887).
,, *alcinous*, in Novit. Zool. 1895. p. 267. t. VI. f. 1-20, 32-38.
,, *alcinous alcinous*, in Klug, *Neue Schmett. Ins. Samml. Berlin* 1836. t. 1 (♂, ♀).
,, *alcinous confusus*, in Novit. Zool. 1895. p. 269.
,, *alcinous loochooanus*, in Novit. Zool. 1896. p. 421.
,, *ambrax*, in Novit. Zool. 1895. p. 354.
,, *ambrax ambrax*, in Dehaan, *Verh. Nat. Gesch. Ned. ovez. bez.* 1840. t. 7. f. 1 (♂). 2 (♀).
,, *antiphates*. in Novit. Zool. 1895. p. 410.
,, *aristeus*, in Novit. Zool. 1895. p. 418.
,, *aristeus anticrates*, in Gray, *Cat. Lep. Ins. B. M.* I. t. 3. f. 3 (1842).
,, *aristeus aristeus*, in Cramer, *Pap. Exot.* IV. t. 318. f. E. F (1782).
,, *aristeus hermocrates*, in *Reise Novara, Lep.* I. t. 12. f. E (1865).
,, *aristeus parmatus*, in Gray, *l.c.* t. 3. f. 2 (1842).
,, *aristolochiae*, in Novit. Zool. 1895. p. 215.
,, *aristolochiae antiphus*, in Donovan, *Ins. of India* t. 15. f. 2 (1800).
,, *aristolochiae aristolochiae*. in Distant, *Rhop. Mal.* 1885. t. 31. f. 6. 7 (as *diphilus*).
,, *aristolochiae austrosundanus*, in Novit. Zool. 1895. p. 249.
,, *bathycles*, in Novit. Zool. 1895. p. 437.
,, *bathycles bathycles*. in *Nov. Act. Ac. Nat. Cur.* 1831. t. 14. f. 6. 7.
,, *bathycles bathycloides*, in *Berl. Ent. Zeitschr.* XXVIII. t. 10. f. 3 (1884).
,, *bathycles chiron*, in *Trans. Linn. Soc. Lond.* XXV. p. 66. note (1865).
,, *bathycles chiron* ab. *chironides*, in *Berl. Ent. Zeitschr.* XXVIII. t. 10. f. 4 (1884).
,, *canopus*, in Novit. Zool. 1895. p. 341.
,, *caunus*, in Novit. Zool. 1895. p. 376.
,, *caunus aegialus*, in Distant, *Rhop. Mal.* 1885. t. 27B. f. 5.
,, *caunus caunus*, in Westwood, *Cab. Or. Ent.* 1848. t. 9. f. 2. 2*.
,, *caunus mendax*, in Haase, *Unters. üb. Mimicry* 1893. t. 8. f. 53.
,, *cloanthus*, in Novit. Zool. 1895. p. 445.
,, *cloanthus cloanthus*, in Westwood, *Arc. Ent.* 1841. t. 11. f. 2.

LIST OF INSECTS MENTIONED IN THIS PAPER.

Acherontia atropos, in Hübner, *Samml. Eur. Schm.* II. *Sphing.* f. 63 (1798-1805).
Callimorpha dominula dominula, in Esper. *Eur. Schm.* IV. t. 83. f. 1. 2 (1786).
,, *dominula persona*, in Hübner, *Samml. Eur. Schm.* III. f. 319-322 (1798—1805).
Euploea rhadamanthus, in Distant, *Rhop. Mal.* 1885. t. 4. f. 4. 5 (as *diocletianus*).
Gonopteryx cleopatra, in Hübner, *Samml. Eur. Schm.* f. 445. 446 (1798—1805).
,, *rhamni*, *ibid.* f. 442-444.
Hepialus humuli hethlandicus, in *Entomol.* 1880. t 3.
,, *humuli humuli*, in Esper, *Eur. Schmett.* IV. t. 80. f. 1 (♂). 2 (♀). (1786).
Ornithoptera, see *Troides*.
Papilio aegeus, in Novit. Zool. 1895. p. 304.
,, *aegeus adrastus*, in *Reise Novara, Lep.* I. t. 16. f. a (1865).
,, *aegeus aegeus*, in Staud. & Schatz, *Exot. Schmett.* I. t. 4 (1884).
,, *aegeus bismarckianus*, in Novit. Zool. 1895. p. 308.
,, *aegeus keianus*, in Novit. Zool. 1896. p. 422.
,, *aegeus ormenus*, in Novit. Zool. 1895. p. 306.
,, *aegeus ormenus* ♂-ab. *ormenus*, in *Voyage Coquille, Ins.* t. 14. f. 3 (1829).
,, *aegeus ormenus* ♂-ab. *othello*, in Novit. Zool. 1894. p. 332. n. 3.
,, *aegeus ormenus* ♂-ab. *pandion*, in *Trans. Linn. Soc. Lond.* XXV. p. 56. n. 72 (1865).
,, *agamemnon*, in Novit. Zool. 1895. p. 417.
,, *agamemnon argynnus*, in *Ann. Mag. N. H.* (6). II. p. 235 (1888).
,, *agamemnon neopommeranius*, in *Berl. Ent. Zeitschr.* XXXI. t. 6. f. 4 (1887).
,, *alcinous*, in Novit. Zool. 1895. p. 267. t. VI. f. 1-20, 32-38.
,, *alcinous alcinous*, in Klug, *Neue Schmett. Ins. Samml. Berlin* 1836. t. 1 (♂, ♀).
,, *alcinous confusus*, in Novit. Zool. 1895. p. 269.
,, *alcinous loochooanus*, in Novit. Zool. 1896. p. 421.
,, *ambrax*, in Novit. Zool. 1895. p. 354.
,, *ambrax ambrax*, in Dehaan, *Verh. Nat. Gesch. Ned. ovez. bez.* 1840. t. 7. f. 1 (♂). 2 (♀).
,, *antiphates*. in Novit. Zool. 1895. p. 410.
,, *aristeus*, in Novit. Zool. 1895. p. 418.
,, *aristeus anticrates*, in Gray, *Cat. Lep. Ins. B. M.* I. t. 3. f. 3 (1842).
,, *aristeus aristeus*, in Cramer, *Pap. Exot.* IV. t. 318. f. E. F (1782).
,, *aristeus hermocrates*, in *Reise Novara, Lep.* I. t. 12. f. E (1865).
,, *aristeus parmatus*, in Gray, *l.c.* t. 3. f. 2 (1842).
,, *aristolochiae*, in Novit. Zool. 1895. p. 215.
,, *aristolochiae antiphus*, in Donovan, *Ins. of India* t. 15. f. 2 (1800).
,, *aristolochiae aristolochiae*. in Distant, *Rhop. Mal.* 1885. t. 31. f. 6. 7 (as *diphilus*).
,, *aristolochiae austrosundanus*, in Novit. Zool. 1895. p. 249.
,, *bathycles*, in Novit. Zool. 1895. p. 437.
,, *bathycles bathycles*. in *Nov. Act. Ac. Nat. Cur.* 1831. t. 14. f. 6. 7.
,, *bathycles bathycloides*, in *Berl. Ent. Zeitschr.* XXVIII. t. 10. f. 3 (1884).
,, *bathycles chiron*, in *Trans. Linn. Soc. Lond.* XXV. p. 66. note (1865).
,, *bathycles chiron* ab. *chironides*, in *Berl. Ent. Zeitschr.* XXVIII. t. 10. f. 4 (1884).
,, *canopus*, in Novit. Zool. 1895. p. 341.
,, *caunus*, in Novit. Zool. 1895. p. 376.
,, *caunus aegialus*, in Distant, *Rhop. Mal.* 1885. t. 27B. f. 5.
,, *caunus caunus*, in Westwood, *Cab. Or. Ent.* 1848. t. 9. f. 2. 2*.
,, *caunus mendax*, in Haase, *Unters. üb. Mimicry* 1893. t. 8. f. 53.
,, *cloanthus*, in Novit. Zool. 1895. p. 445.
,, *cloanthus cloanthus*, in Westwood, *Arc. Ent.* 1841. t. 11. f. 2.

Papilio cloanthus clymenus, in Leech, *Butt. from China and Japan* 1893. t. 32. f. 2.
,, *cloanthus sumatranus*, in *Iris* VI. 1891. p. 27.
,, *clytia*, in Novit. Zool. 1895. p. 364.
,, *deiphobus*, in Clerck, *Icones* II. t. 25. f. 1 (1764).
,, *deiphontes*, in Staud. & Schatz, *Exot. Schmett.* I. t. 5 (♂, ♀) (1884).
,, *deipylus*, in *Verh. z. b. Ges. Wien.* 1864. p. 323. n. 155.
,, *depilis*, in Novit. Zool. 1895. p. 339.
,, *depilis depilis*, in Novit. Zool. 1895. p. 340 (N. Britain, *nec* N. Ireland).
,, *depilis novohibernicus*, in Novit. Zool. 1896. p. 422.
,, *echidna*, in Dehaan, *l.c.* t. 8. f. 6.
,, *euchenor*, in Novit. Zool. 1895. p. 339.
,, *euchenor euchenor*, in *Voyage Coquille, Ins.* t. 13. f. 3 (1829).
,, *euchenor godarti*, in *Ann. Sc. Phys. Nat. Lyon.* 1856. p. 398 (♂, *nec* ♀).
,, *euchenor obsolescens*, in Novit. Zool. 1895. p. 339.
,, *eurypylus*, in Novit. Zool. 1895. p. 429.
,, *gambrisius*, in Cramer, *l.c.* II. t. 157. f. A. B (1779).
,, *inopinatus*, in Smith & Kirby, *Rhop. Exot., Pap.* 1893. t. 12. f. 1 (♂). 2 (♀).
,, *lowi*, in *P. Z. S.* 1873. t. 33. f. 6 (♂).
,, *macfarlanei*, in Novit. Zool. 1895. p. 446.
,, *machaon*, in Novit. Zool. 1895. p. 272.
,, *machaon flavus*, in Tutt, *Brit. Butt.* 1896. p. 218; as *machaon* in Barrett, *Lep. Brit. Isl.* 1893. t. 1. f. 1. 1a.
,, *machaon hippocrates*, in Pryer, *Rhop. Nih.* 1886. t. 1. f. 1a. 1b.
,, *machaon machaon*, in Roesel, *Ins. Belust.* I. 2. 1746. t. 1.
,, *machaon sphyrus*, in Novit. Zool. 1895. p. 275.
,, *mandarinus*, in Novit. Zool. 1895. p. 408.
,, *mayo*, in *P. Z. S.* 1873. t. 63. f. 1 (♂).
,, *memnon*, in Novit. Zool. 1895. p. 312.
,, *memnon agenor*, in Distant, *Rhop. Mal.* 1885. t. 27b. f. 7; t. 28. f. 1-7; t. 29 f. 1. 4. 5; under various names.
,, *memnon memnon*, in *Trans. Linn. Soc. Lond.* XXV. t. 1. f. 1. 2. 3. 4 (1865).
,, *nomius*, in Novit. Zool. 1895. p. 421.
,, *paradoxus*, in Novit. Zool. 1895. p. 371.
,, *paron*, in Smith & Kirby, *Rhop. Exot., Pap.* 1893. t. 31. f. 3. 4.
,, *peranthus*, in Novit. Zool. 1895. p. 391.
,, *phestus*, in *Voyage Coquille, Ins*1829. t. 14. f. 2. A. B.
,, *podalirius*, in Novit. Zool. 1895. p. 402.
,, *polytes*, in Novit. Zool. 1895. p. 343.
,, *polytes alcindor*, in Oberthür, *Et. d'Ent.* IV. 1879. t. 6. f. 4 (♀); Novit. Zool. 1895. p. 350.
,, *polytes alphenor*, in Cramer, *l.c.* I. t. 90. f. B (♀) (1779); ♂ as *ledebouria* in Kotzebue's *Reise* III. t. 3. f. 7 (1821).
,, *polytes borealis*, in Novit. Zool. 1895. p. 348.
,, *polytes borealis* ab. *thibetanus*, in Oberthür, *l.c.* XIII. 1886. p. 14.
,, *polytes nicanor*, in Staud. & Schatz, *Exot. Schmett.* I. 1884. t. 3 (♂, ♀).
,, *polytes nikobarus*, in *Verh. z. b. Ges. Wien.* 1862. p. 483. n. 112.
,, *polytes perversus*, in Novit. Zool. 1895. p. 353.
,, *polytes polytes*, in Distant, *l.c.* t. 33. f. 7-10.
,, *polytes theseus*, in *Trans. Linn. Soc. Lond.* XXV. t. 2. f. 2. 4. 7 (1865).
,, *rhesus*, in Eimer, *Artb. u. Verwandtsch. Schmett.* 1889. t. 4. f. 6.
,, *rumanzovius*, in Kotzebue's *Reise* III. 1821. t. 2. f. 1a. 4b (♀); ♂ as *krusensternia*, *ibid.* t. 3. f. 5a. 5b.

Papilio cloanthus clymenus, in Leech, *Butt. from China and Japan* 1893. t. 32. f. 2.
,, *cloanthus sumatranus*, in *Iris* VI. 1891. p. 27.
,, *clytia*, in Novit. Zool. 1895. p. 364.
,, *deiphobus*, in Clerck, *Icones* II. t. 25. f. 1 (1764).
,, *deiphontes*, in Staud. & Schatz, *Exot. Schmett.* I. t. 5 (♂, ♀) (1884).
,, *deipylus*, in *Verh. z. b. Ges. Wien.* 1864. p. 323. n. 155.
,, *depilis*, in Novit. Zool. 1895. p. 339.
,, *depilis depilis*, in Novit. Zool. 1895. p. 340 (N. Britain, *nec* N. Ireland).
,, *depilis novohibernicus*, in Novit. Zool. 1896. p. 422.
,, *echidna*, in Dehaan, *l.c.* t. 8. f. 6.
,, *euchenor*, in Novit. Zool. 1895. p. 339.
,, *euchenor euchenor*, in *Voyage Coquille, Ins.* t. 13. f. 3 (1829).
,, *euchenor godarti*, in *Ann. Sc. Phys. Nat. Lyon.* 1856. p. 398 (♂, *nec* ♀).
,, *euchenor obsolescens*, in Novit. Zool. 1895. p. 339.
,, *eurypylus*, in Novit. Zool. 1895. p. 429.
,, *gambrisius*, in Cramer, *l.c.* II. t. 157. f. A. B (1779).
,, *inopinatus*. in Smith & Kirby. *Rhop. Exot., Pap.* 1893. t. 12. f. 1 (♂). 2 (♀).
,, *lowi*, in *P. Z. S.* 1873. t. 33. f. 6 (♂).
,, *macfarlanei*, in Novit. Zool. 1895. p. 446.
,, *machaon*, in Novit. Zool. 1895. p. 272.
,, *machaon flavus*, in Tutt, *Brit. Butt.* 1896. p. 218; as *machaon* in Barrett, *Lep. Brit. Isl.* 1893. t. 1. f. 1. 1a.
,, *machaon hippocrates*, in Pryer, *Rhop. Nih.* 1886. t. 1. f. 1a. 1b.
,, *machaon machaon*, in Roesel, *Ins. Belust.* I. 2. 1746. t. 1.
,, *machaon sphyrus*, in Novit. Zool. 1895. p. 275.
,, *mandarinus*, in Novit. Zool. 1895. p. 408.
,, *mayo*, in *P. Z. S.* 1873. t. 63. f. 1 (♂).
,, *memnon*, in Novit. Zool. 1895. p. 312.
,, *memnon agenor*, in Distant, *Rhop. Mal.* 1885. t. 27b. f. 7; t. 28. f. 1-7; t. 29 f. 1. 4. 5; under various names.
,, *memnon memnon*, in *Trans. Linn. Soc. Lond.* XXV. t. 1. f. 1. 2. 3. 4 (1865).
,, *nomius*, in Novit. Zool. 1895. p. 421.
,, *paradoxus*, in Novit. Zool. 1895. p. 371.
,, *paron*, in Smith & Kirby, *Rhop. Exot., Pap.* 1893. t. 31. f. 3. 4.
,, *peranthus*, in Novit. Zool. 1895. p. 391.
,, *phestus*, in *Voyage Coquille, Ins*1829. t. 14. f. 2. A. B.
,, *podalirius*, in Novit. Zool. 1895. p. 402.
,, *polytes*, in Novit. Zool. 1895. p. 343.
,, *polytes alcindor*, in Oberthür, *Et. d'Ent.* IV. 1879. t. 6. f. 4 (♀); Novit. Zool. 1895. p. 350.
,, *polytes alphenor*, in Cramer, *l.c.* I. t. 90. f. B (♀) (1779); ♂ as *ledebouria* in Kotzebue's *Reise* III. t. 3. f. 7 (1821).
,, *polytes borealis*, in Novit. Zool. 1895. p. 348.
,, *polytes borealis* ab. *thibetanus*, in Oberthür, *l.c.* XIII. 1886. p. 14.
,, *polytes nicanor*, in Staud. & Schatz, *Exot. Schmett.* I. 1884. t. 3 (♂, ♀).
,, *polytes nikobarus*, in *Verh. z. b. Ges. Wien.* 1862. p. 483. n. 112.
,, *polytes perversus*, in Novit. Zool. 1895. p. 353.
,, *polytes polytes*, in Distant, *l.c.* t. 33. f. 7-10.
,, *polytes theseus*, in *Trans. Linn. Soc. Lond.* XXV. t. 2. f. 2. 4. 7 (1865).
,, *rhesus*, in Eimer, *Artb. u. Verwandtsch. Schmett.* 1889. t. 4. f. 6.
,, *rumanzovius*, in Kotzebue's *Reise* III. 1821. t. 2. f. 1a. 4b (♀); ♂ as *krusensternia*, *ibid.* t. 3. f. 5a. 5b.

Papilio sarpedon, in Novit. Zool. 1895. p. 441.
,, *sarpedon adonarensis*, Novit. Zool. 1896. p. 324.
,, *sarpedon anthedon*, in Staud. & Schatz, *Exot. Schmett.* I. 1884. t. 6.
,, *sarpedon choredon*, in Scott, *Austr. Lep.* II. 1890. t. 17.
,, *sarpedon dodingensis*, in Novit. Zool. 1896. p. 323.
,, *sarpedon impar*, in Novit. Zool. 1895. p. 443.
,, *sarpedon imparilis*, in Novit. Zool. 1895. p. 443.
,, *sarpedon isander*, in Smith & Kirby, *Rhop. Exot.* I. 1888. *Pap.* t. 6. f. 3.
,, *sarpedon jugans*, in Novit. Zool. 1896. p. 324.
,, *sarpedon milon*, in *Trans. Linn. Soc. Lond.* XXV. 1865. t. 7. f. 2 (as *miletus*).
,, *sarpedon monticolus*, in *Societas Entomol.* 1896. p. 20.
,, *sarpedon sarpedon*, in Distant, *Rhop. Mal.* 1885. t. 22. f. 6.
,, *sarpedon semifasciatus*, in *Trans. Ent. Soc. Lond.* 1889. t. 7. f. 2 (as *sarpedon* var.)
,, *sarpedon teredon*, in Moore, *Lep. Ceyl.* I. 1882. t. 62. f. 1.
,, *sarpedon teredon* ab. *thermodusa*, in *P. Z. S.* 1885. p. 146. n. 145.
,, *sarpedon timorensis*, in Novit. Zool. 1896. p. 323.
,, *semperi*, in Semper. *Tagf. Philipp.* 18.
,, *tydeus*, in *Reise Novara*, *Lep.* I. 1865. t. 16. f. c; t. 17. f. a.
Pieris rapae ab. loc. *novangliae*, in Scudder, *Butt. New Engl.* II. 1889. p. 1207.
Plusiotis aurora ab. *aurora*, in *P. Z. S.* 1875. t. 23. f. 7.
,, *aurora* ab. *chrysopedila*, in *Biol. Centr. Amer.*, *Col.* II. t. 16. f. 12 (1888).
Polyommatus phlaeas, in Hübner, *Samml. Eur. Schm.* I. f. 362. 363 (1798—1805).
Troides croesus, in *P. Z. S.* 1859. t. 68. 69.
,, *lydius*, in *Reise Novara*, *Lep.* I. 1865. t. 3. f. a. b.
,, *priamus*, in Novit. Zool. 1895. p. 183.
,, *priamus euphorion*, in Rippon, *Icon. Ornith.* 1890. t. 2.
,, *priamus poseidon*, in Westwood, *Cab. Or. Ent.* 1848. t. 11 (♂).
,, *priamus priamus*, in Cramer, *Pap. Ex.* I. 1775. t. 23. f. A. B.
,, *priamus urvillianus*, in *Voyage Coquille* 1829. *Ins.* t. 13. f. 1. 2.
,, *tithonus*, in Dehaan, *l.c.* t. 1. f. 1.

Papilio sarpedon, in Novit. Zool. 1895. p. 441.
,, *sarpedon adonarensis*, Novit. Zool. 1896. p. 324.
,, *sarpedon anthedon*, in Staud. & Schatz, *Exot. Schmett.* I. 1884. t. 6.
,, *sarpedon choredon*, in Scott, *Austr. Lep.* II. 1890. t. 17.
,, *sarpedon dodingensis*, in Novit. Zool. 1896. p. 323.
,, *sarpedon impar*, in Novit. Zool. 1895. p. 443.
,, *sarpedon imparilis*, in Novit. Zool. 1895. p. 443.
,, *sarpedon isander*, in Smith & Kirby, *Rhop. Exot.* I. 1888. *Pap.* t. 6. f. 3.
,, *sarpedon jugans*, in Novit. Zool. 1896. p. 324.
,, *sarpedon milon*, in *Trans. Linn. Soc. Lond.* XXV. 1865. t. 7. f. 2 (as *miletus*).
,, *sarpedon monticolus*, in *Societas Entomol.* 1896. p. 20.
,, *sarpedon sarpedon*, in Distant, *Rhop. Mal.* 1885. t. 22. f. 6.
,, *sarpedon semifasciatus*, in *Trans. Ent. Soc. Lond.* 1889. t. 7. f. 2 (as *sarpedon* var.)
,, *sarpedon teredon*, in Moore, *Lep. Ceyl.* I. 1882. t. 62. f. 1.
,, *sarpedon teredon* ab. *thermodusa*, in *P. Z. S.* 1885. p. 146. n. 145.
,, *sarpedon timorensis*, in Novit. Zool. 1896. p. 323.
,, *semperi*, in Semper. *Tagf. Philipp.* 18.
,, *tydeus*, in *Reise Novara, Lep.* I. 1865. t. 16. f. c; t. 17. f. a.
Pieris rapae ab. loc. *novangliae*, in Scudder, *Butt. New Engl.* II. 1889. p. 1207.
Plusiotis aurora ab. *aurora*, in *P. Z. S.* 1875. t. 23. f. 7.
,, *aurora* ab. *chrysopedila*, in *Biol. Centr. Amer.*, *Col.* II. t. 16. f. 12 (1888).
Polyommatus phlaeas, in Hübner, *Samml. Eur. Schm.* I. f. 362. 363 (1798—1805).
Troides croesus, in *P. Z. S.* 1859. t. 68. 69.
,, *lydius*, in *Reise Novara, Lep.* I. 1865. t. 3. f. a. b.
,, *priamus*, in Novit. Zool. 1895. p. 183.
,, *priamus euphorion*, in Rippon, *Icon. Ornith.* 1890. t. 2.
,, *priamus poseidon*, in Westwood, *Cab. Or. Ent.* 1848. t. 11 (♂).
,, *priamus priamus*, in Cramer, *Pap. Ex.* I. 1775. t. 23. f. A. B.
,, *priamus urvillianus*, in *Voyage Coquille* 1829. *Ins.* t. 13. f. 1. 2.
,, *tithonus*, in Dehaan, *l.c.* t. 1. f. 1.